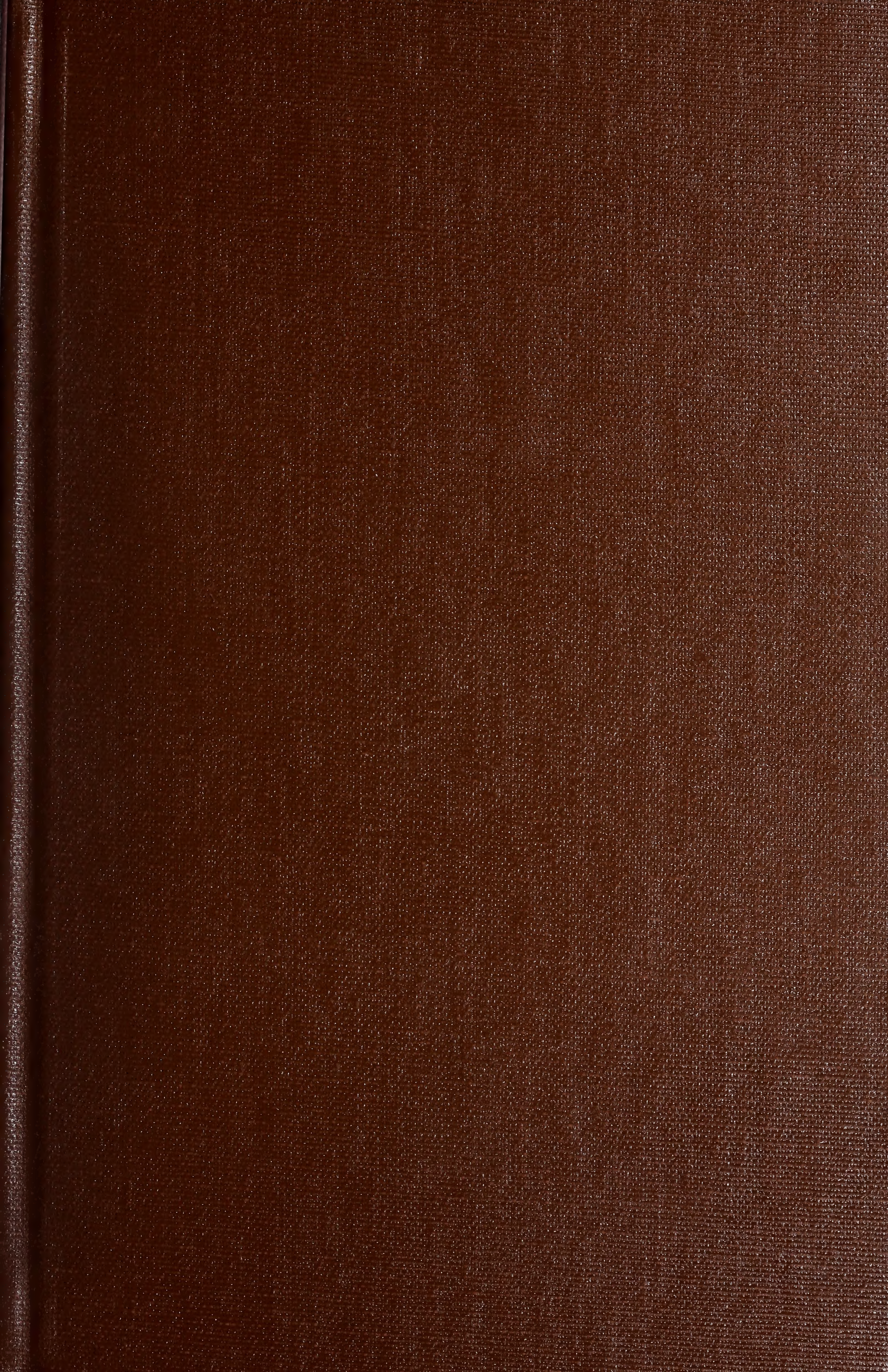
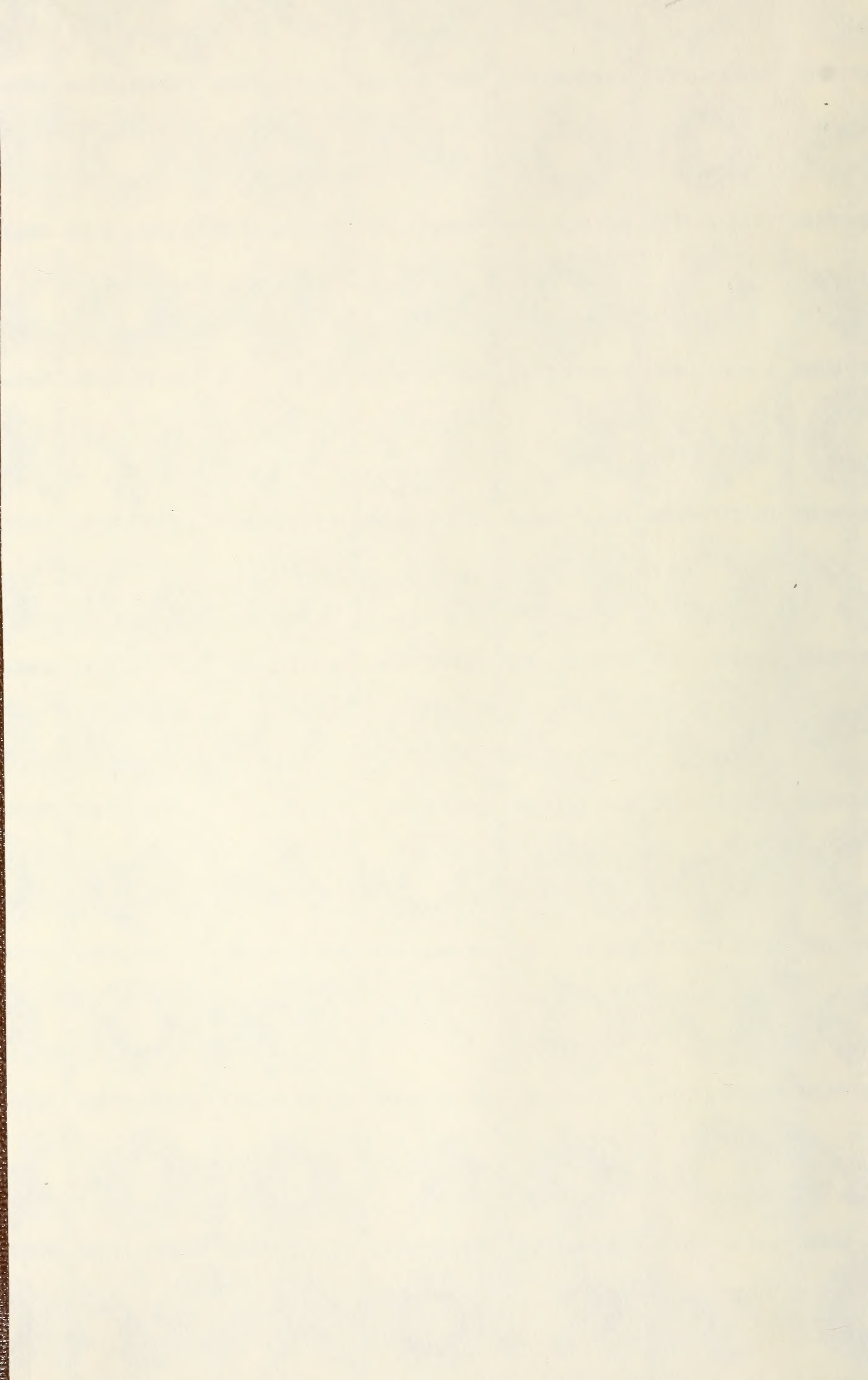








ZEITSCHRIFT FÜR SÄUGETIERKUNDE

INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Organ der Deutschen Gesellschaft für Säugetierkunde

Volume 53, 1988 ISSN 0044–3468

Mit 176 Abbildungen



Verlag Paul Parey Hamburg und Berlin

Wissenschaftliche Originalarbeiten

Wissenschaftliche Kurzmitteilungen

Bekanntmachungen

Buchbesprechungen

This journal is covered by Biosciences Information Service of Biological Abstracts, and by Current Contents (Series Agriculture, Biology, and Environmental Sciences) of Institute for Scientific Information

ISSN 0044-3468 53 (1–6) 1–384 (1988)

Vol. 53 (1), 1–64, Februar 1988 ISSN 0044-3468 C 21274 F

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Fortsetzung 3. Umschlagseite

 Verlag: Paul Parey, Hamburg und Berlin. Anschriften: Spitalerstr. 12, D-2000 Hamburg 1; Lindenstr. 44–47, D-1000 Berlin 61. – Printed in Germany by Westholsteinische Verlagsdruckerei Boyens & Co., D-2240 Heide/Holst.

Z. Säugetierkunde 53 (1988) 1–6

ISSN 0044-3468

Reproductive reorganization in incomplete groups of the common marmoset *(Callithrix jacchus)* under laboratory conditions

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Receipt of Ms. 22. 12. 1986

Abstract

Incomplete groups of *Callithrix jacchus* which exclusively consist of genetically related members show a rather considerable frequency of inbreeding. Therefore, the incest taboo seems to be realized at a very low level, eventually due to the laboratory environment. *C. jacchus* daughters are able to conceive in the presence of their mother. This result confirms to some extent the previous assumption upon a hierarchy dependent monogamy in the common marmoset. The reproductive reorganization of groups which have genetically unrelated members exclusively relies on these animals.

Introduction

Most authors believe marmosets to be monogamous (e.g. Rothe 1979). Bischof (1985) describes their mating and reproductive organization as 'aristogamy' since only the highest ranking group members (= parents) are allowed to interact sexually and to reproduce. Only from one species, i.e. *Saguinus fuscicollis,* we have some information from field observations that tamarins might be organized in cooperative polyandrous groups (Terborgh and Goldizen 1985).

Following the loss of one or both parent(s) monogamous groups are at first confronted with a temporary or even permanent loss of their ability to reproduce. The reproductive reorganization can be achieved by a subsequent breeding of the remaining parent with one of the adult offspring, however, undergoing by this all risks and disadvantages of inbreeding. On the other hand, reproduction can be continued by integration of a strange adult conspecific.

Reproduction of the group ceases completely if neither inbreeding nor integration of a strange conspecific occurs. The same is true if the group dissolves by emigration of single family members or even subgroups.

Up to now we do not have any detailed information on the strategy free ranging groups will follow when afflicted by the loss of one or both parents. Under laboratory conditions incomplete families as a rule cannot decide for a strategy of reproductive reorganization which includes gene flow by integration/immigration of a strange conspecific. That mode of regaining reproductive ability is only possible by interference of the investigator (Rothe et al., in press).

In this paper we confine to a description of inbreeding in the common marmoset and mechanisms of its avoidance.

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Material and methods

The data were taken from the diary of our marmoset colony and from observations during the daily routine work (e.g. observations on sexual behaviour). Informations on stability/instability of the respective families exclusively refer to those contexts which led to the expulsion or removal of one or even more group members (for details see ROTHE et al., in press).

We analyzed 20 *Callithrix jacchus* groups which lived at least for another two months following the loss of their mother or at least two months after the last delivery of the mother in groups, whose α-male has died. The period of two months has been determined empirically, that is, we have made the observation that groups experienced dissolution shortly after the death of the α-female or the α-male (some days up to half a month). Therefore the chance to observe sexual behaviour has been very low. Furthermore all groups we describe in this paper had adult and fertile offspring.

According to group composition we distinguish three categories: 1. groups which consisted of related members only (parents and their offspring) (n = 15). 2. groups with nonrelated members: a. by integration of hand- and/or foster mother reared infants/juveniles (n = 4); b. by integration of an adult male in an all-female group (mother and four daughters) (n = 1).

Additional informations are given on two special groups which showed different basic parameters compared to the other families, but which revealed inbreeding as well.

Results

With the exception of the special groups six families (30 %) showed further reproduction (one to three litters). In two families we at least observed sexual behaviour.

Groups with related members exclusively (n = 15)

Reproduction continued in four groups. One of these became unstable after the loss of a parent whereas this was true for 75 % of those incomplete families which have ceased reproduction (Table 1). One group experienced unstable periods following the next delivery (Table 1). Table 1 refers to the group composition as well as to the dates of the breeding females' conceptions. It is quite obvious that the unstable groups showed the longest break in reproduction. Group M is characterized by a special history (s. Table 1). The α-female has been sick for the last six months preceding her death. During that time she got rather regularly medical therapy. Already during her mother's illness an adult daughter has been impregnated by her father. The resulting delivery occurred three months following the α-female's death. EPPLE (1967) refers to a similar event in her *C. jacchus* colony.

Groups with genetically unrelated members (n = 5)

One group which had altogether three (2.1) integrated members (hand and foster mother reared infants) did neither show sexual nor reproductive behaviour. This group was remarkably unstable, however, we also recruted group members for pair formation. In two groups we observed copulations. Both families have been unstable periodically. After the death of the α-male copulations occurred between the α-female and one of the genetically unrelated, meanwhile adult male group members. However, we could not detect any sexual intercourse between the mother and her adult sons. In another group a young female (11 months old) which had been integrated as infant into this family became pregnant after 45 days. This female was considerably younger than an adult daughter of the α-male, with whom the male did not interact sexually. In a third group we observed copulations between an adult male which has been integrated into the family some months ago and one of the oldest females shortly after the death of the α-female. About seven months after the death of the mother the female gave birth to triplets (see also ROTHE et al., in press).

Table 1. **Groups with related members exclusively**

group	loss	α-f pregnant	age of group (mo)	sex ratio	age/sex classes: ad	yad	sub	iuv	inf	expulsion of GM: before loss n	days	after loss n	days	expulsion after birth: n	days after loss	days after birth	conception: days after loss	age of female (mo)	birth n	remarks
M	α-f	--	33	6.2	$\underline{m}$*	mf*mf	mm	m	-	-	--	-	--	2	100 174	8 82	--	20	2	conception approx. 50 days before loss of α-f
N	α-f	--	36	3.2	$\underline{m}$*	mf*	-	-	-	-	--	-	--	-	--	--	108	26	1	father unknown, group dissolved
C	α-f	--	97.5	5.6	$\underline{f}$m*m $\underline{m}$ff* m	ff	mf	-	-	3	112 77 43	3	2 152 164	-	--	--	187	75	3	last delivery one month before loss of α-m; at first expulsion hunter caught; two GM recruted
CF	α-m	--	--	1.1	-	m*f*	-	-	-	-	--	-	--	-	--	--	26	20	1	mf descended from special group, see text; α-f died 10 mo before; mf not yet fertile
B2	α-m/f	--	66	3.6	fmf	ffff	mm	-	-	-	--	4	8 89 107	-	--	--	--	--	-	group was divided after fighting; on day 8 two GM expelled; comp. diss.: 10 mo
F1	α-m/f	--	29	1.2	f	fm	-	-	-	2	12 6	-	--	-	--	--	--	--	-	ad f daughter from F; α-f died 7 days after loss of α-m and some GM; comp. diss.: 2.5 mo
G	α-f	--	29	4.1	$\underline{m}$	mmf	-	-	-	-	--	2	9 48	-	--	--	--	--	-	comp. diss.: 24 mo
J	α-f	--	51	4.3	$\underline{m}$m	mfmff	-	-	-	-	--	1	5	-	--	--	--	--	-	at first expulsion hunter caught; α-m died two mo after α-f; comp. diss.: 6 mo
M1	α-f	--	16	3.2	$\underline{m}$m	-	mf	f	-	-	--	1	19	-	--	--	--	--	-	ad m son from M; at first expulsion hunter caught; comp. diss.: 10 mo
X	α-f	--	16	3.2	$\underline{m}$	-	ff	-	mm	-	--	-	--	-	--	--	--	--	-	comp. diss.: 24 mo
CB	α-f	--	32.5	3.6	$\underline{m}$	ffmf	mf	ff	-	-	--	3	3 5	-	--	--	--	--	-	on day 5 two hunters caught; one GM recruted; comp. diss.: 11,5 mo
CC	α-f	--	32.5	2.4	$\underline{m}$	ffff	-	m	-	-	--	-	--	-	--	--	--	--	-	after 14,5 mo m and one f recruted; comp. diss.: 17 mo
CP	α-f	--	22.5	2.2	$\underline{m}$	ff	-	m	-	1	8	-	--	-	--	--	--	--	-	comp. diss.: 11 mo
CE	α-m	x	51	8.4	$\underline{f}$mm	mffmm mm	mf	-	-	-	--	-	--	4	123 126 170 171	122 125 169 170	--	--	1	delivery one day after loss of α-m; comp. diss.: 9,5 mo
V	α-m	x	20	3.4	$\underline{f}$	ff	mf	mm	-	-	--	-	--	1	151	92	--	--	1	after 12 days yad ff recruted; delivery 59 days after loss; comp. diss.: 5.5 mo

mo - month(s); m - male; f - female; $\underline{m}$ - α-animal before loss; * - new α-animal; GM - group member(s); comp. diss. - complete dissolution; ad > 35 mo; yad - 35 to 15 mo; sub - 15 to 10 mo; iuv - 10 to 5 mo; inf < 5 mo; expulsions only up to approx. 170 days before/after loss/birth included (one interbirth-interval).

Table 2. **Groups with non-related members and special groups[1]**

group	loss	α-f preg-nant	age of group (mo)	sex ratio	age/sex classes ad	yad	sub	iuv	inf	expulsion of GM: before loss n	days	after loss n	days	expulsion: after birth: n	days after loss	days after birth	sex behav. observed: days after loss	days after birth	conception: days after loss	age of female (mo)	birth n
C1[2]	α-f	--	17	4.2	m*m	-	f	f+*m+ m+	-	3	7 4	-	--	-	--	--	--	--	45	11	2
CRxU[3]	α-f	--	6	1.4	m*	f*f	ff	-	-	-	--	1	45	1	209	3	1	--	62	18	1
R[4]	α-m	x	26	6.2	f*	mm+* m+m+f+	mm	-	-	1	23	-	--	-	--	--	210	81	--	--	1
CJ[5]	α-m	x	39	3.8	f*	ff*f m+*	mf	ff	mf	-	--	-	--	1	210	103	164	65	--	--	1
L[6]	α-f	--	19	6.4	m	mff	m+m m+m+	mf	-	-	--	-	--	-	--	--	--	--	--	--	-
F[7]	α-m	x	25.5	1.6	f*	mf	fff	f	-	1	--	-	--	1	261	56	222	17	61	60	6

mo - month(s); m - male; f - female; m - α-animal before loss; * - new α-animal or partner of sexual interaction; + - integrated hand- and/or foster mother reared iuvenile or infant; GM - group member; comp. diss. - complete dissolution; ad > 35 mo; yad - 35 to 15 mo; sub - 15 to 10 mo; iuv - 10 to 5 mo; inf < 5 mo; expulsions only up to approx. 170 days after/before loss/birth included (one interbirth-interval).

[1]) second special group see text and table 2 group CF;
[2]) ad m brother of m; after first delivery group was dissolved except α-animals;
[3]) m 6 mo before loss of α-f integrated, 'stepfather';
[4]) delivery 131 days after loss; group became unstable after approx. 190 days;
[5]) delivery 107 days after loss; f became ill after delivery;
[6]) shortly after loss 1 GM recruted; after approx. 200 days the group became very unstable; 2 hunter caught; 3 other GM recruted; comp. diss.: 14 mo
[7]) special group; α-male expelled; 57 days after loss abortion, not included; conception 4 days after abortion.

Special groups (n = 2)

In one group the father has been so severely attacked by his son that he had to be removed from the family. He died some minutes later due to a severe shock. We do not know why the father has been attacked. Subsequently the son interacted sexually with his mother. This pair produced altogether six litters. In the second case a sexually experienced male (father of 13 litters) got for social companion one of his adult daughters (mother of 7 litters). The female gave birth to male/female litter (see also FRENCH et al. 1984 for *S. oedipus*) which reproduced as well after removal of their parents (Table 1).

Discussion

The rather high frequency of inbreeding in incomplete groups cannot be interpreted as a mere accidental event. It is striking how often the groups violate the incest taboo, supposed such a phenomenon actually exists. The expulsion of the α-male in Gr. F (s. Table 2) (a similar situation was observed by SPICHIGER-CARLSSON, 1982) may indicate that the incest taboo is only weakly realized in the common marmoset, and eventually influenced by the laboratory condition.

No less important seems to us the sexual interactions of a female with her father and the onset of pregnancy whilst the mother was sick and had to be treated medically (see also EPPLE 1967). This observation confirms the findings of ABBOTT (1984) and EVANS and HODGES (1984) according to which the daughters may ovulate in the presence of their mother. Besides this the mere physical presence of their mother (= highest ranking female in the family) does not seem to be sufficient to prevent sexual behaviour of the α-male with his daughter(s). The result of this 'longterm study' contrasts to the observations in a 'shortterm study' of ANZENBERGER (1983), in which the presence of the mother and her offspring prevented sexual behaviour of the father and a strange female in a neighbouring cage, to which only the father and the strange female had access. However, we cannot exclude that the sickness of the α-female might have influenced the result, for example due to the eventuel loss of her α-status because of her physical inability. On the other hand ROTHES (1974) hypothesis that marmosets are monogamous by status and not by emotional bond would be confirmed by that event.

Most striking to us has been the fact that in groups with unrelated members the reproductive reorganization was not incestuous but was based on the integration of the genetically unrelated group members, even when they were younger than the offspring of the remaining parent. We had, however, to prove, whether there has possibly existed a dominance-subordination relationship between the integrated and the family-born group members. In this case the avoidance of inbreeding could only be interpreted as a secondary phenomenon. But if incest avoidance must be regarded as a primary event, then the cognitive capacity of the common marmoset must be highly valued, especially since no group odor could be made responsible for that result (EPPLE, pers. comm.), except it would be genetically determined by a single Mendelian gene locus. To what extent young females experience an accelerated sexual maturation when becoming α-female cannot be answered at the moment (see also TARDIF 1984).

We do not know whether infant transfer and/or infant-emigration/-immigration can be regarded as a regular event in the life of a marmoset group in order to offer a proper strategy for the reproductive reorganization of an uncomplete family. However, DAWSON (1976) observed a rather frequent migration of juvenile *Saguinus oedipus geoffroyi* between neighbouring groups. At least in this tamarin species infant transfer seems to be a regular behaviour in the natural habitat.

Zusammenfassung

Reproduktive Reorganisation in unvollständigen Gruppen des Weißbüscheläffchens (Callithrix jacchus) unter Laborbedingungen

Die vorliegende Arbeit beschreibt Inzucht und deren Vermeidung in unvollständigen *Callithrix jacchus*-Gruppen. Untersucht wurden 20 Gruppen, die in drei Kategorien gegliedert wurden: 1. Gruppen, die ausschließlich verwandte Mitglieder enthalten; 2. Gruppen mit genetisch fremden Tieren a. entweder durch Integration infantiler/juveniler Tiere oder b. durch Integration eines adulten fremden Männchens in eine Weibchen-Gruppe (Mutter und vier Töchter). Insgesamt sechs Gruppen setzten die Reproduktion nach Verlust eines Elters fort. Die relativ große Anzahl von Familien (4 von 15 Gruppen), in denen nach Verlust des Elters Inzucht auftrat, kann nicht mehr als ein rein zufälliges Ereignis gewertet werden. Sehr auffällig ist die Einbeziehung der genetisch nicht verwandten Tiere in die reproduktive Reorganisation, in solchen Gruppen (n = 5), in die genetisch fremde Tiere integriert worden sind.

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Z. Säugetierkunde 53 (1988) 7–10

ISSN 0044-3468

Parent-offspring correlations for growth and reproduction in the vole *Clethrionomus glareolus* in relation to the Chitty Hypothesis

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Receipt of Ms. 13. 11. 1986

Abstract

Studied in laboratory correlations between parents and offspring for weights and reproductive parameters in voles *Clethrionomys glareolus* from a non-cyclic population. Weight correlations were significantly positive in males and negative in females. Reproductive parameters correlated negatively. The latter correlations could be analysed further and be interpreted as due to a negative maternal effect. These findings contradict the Chitty Hypothesis of population regulation but may explain cyclic variations in weight and reproduction if external factors drive the cycles.

Introduction

Microtine cycles are characterized by small animals with high reproductive output during the increasing phase and large, slowly-reproducing animals at peaks. However, small adult animals with low reproduction occur during the declining phase (Krebs and Myers 1974; Taitt and Krebs 1985).

The Chitty Hypothesis (Chitty 1967, 1970, cf. also Krebs 1978), predicting regular genetic changes with cyclic fluctuations, has had a profound impact in explaining such morphological and reproductive variations. It states that timid, slowly-growing but high-reproducing animals are favoured in sparse and increasing pupulations whereas aggressive, large but slowly-reproducing animals are favoured in dense or peak populations. This mashinery should drive the cycles. Body growth and reproductive rates should thus be mainly genetically determined in microtine populations; body size and reproductive output should be closely correlated between parents and offspring. Animals caught in various population phases and brought to a laboratory should retain such correlations if there is low or random (density-independent) selection in the laboratory. These predictions were examined on the bank vole *Clethrionomys glareolus* which appears in both cyclic and non-cyclic populations in Sweden (Hansson and Henttonen 1985a).

Methods

The study was performed on animals which were bred for other reasons (Hansson and Henttonen 1985b; Hansson 1986) under laboratory conditions. The founding animals were taken from a clearly non-cyclic population in south Sweden (Hansson and Henttonen 1985a). Thus, it was possible to evaluate parent-offspring relations with regard to the pattern of population dynamics. The data were examined according to the rules of quantitative genetics but the relationships were mainly expressed as correlations (cf. Millar 1983) since certain prerequisites for heritability analysis may not have been present.

Bank voles were caught in live traps at Revinge (56° N) in 1980–83. The animals were kept as monogamous pairs after capture so the low mortality (19 and 8 % per year for wild-caught and

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laboratory-born animals respectively) was not density-dependent. The voles were caught in early autumn as young animals and kept on constant food (laboratory mouse pellets) and at a constant temperature (20 °C) for one year or until reproduction ended. Young of these animals, born in late summer-early autumn, were kept as monogamous pairs from an age of four months under the same laboratory conditions. Males were weighed every second week and the maximum weights recorded for each individual was used for the computations. In females, pregnancies caused exceptional weights so instead the weight one month before the first parturition was used. The length of pregnancy is ca 20 days in this species. Times of first parturition, litter sizes and number of litters as well as the total number of weaned young were recorded for all field-caught females (P) and their female offspring (F_1). Correlations were examined between weights and reproductive parameters of field-caught animals and the corresponding means of their laboratory-born offspring (Falconer 1981).

Results and discussion

Males showed a strong positive correlation in weights between parents and offspring (Table 1). Females showed a negative correlation, on the border of significance, for the same relationship. The number of litters, number of weaned young, mean litter size and start of reproduction were all consistently but non-significantly negatively related between female parents and offspring (Table 2).

Table 1. **Correlations between maximum body weight (see text for estimation) of P and F_1 *Clethrionomys glareolus***

Sex	N	r	P
Males	12	0.81	<0.01
Females	12	−0.52	~ 0.05

There were thus clearly positive parent-offspring relationships in the body weights of the males. The mean weight ($\bar{x} \pm SD$) of parent (P) males was 24.3 ± 2.4 g and of offspring (F_1) males 23.8 ± 3.0 g so there was no significant change due to laboratory breeding. These relations have to be interpreted as genetic as no sources of error would cause a change in that direction for males (cf. below for females). The regression coefficients ($b \pm SE$) were 1.02 ± 0.24. According to Falconer (1981), this indicates a very high level of heritability. The generally negative relations in both body weights and reproductive parameters between female parents and offspring have to be interpreted as "a negative maternal effect" in analogy with Leamy (1981) and Millar (1983). Both these authors got consistent but low and often non-significant negative correlations in these parameters for both *Peromyscus leucopus* and *P. maniculatus.* They suggested that these negative correlations were due to well-fed females giving birth to large litters, where however each young had a low body weight. The female young were supposed to retain a comparatively low body weight as adults, to reproduce late and to produce small litters.

Table 2. **Correlations between reproductive parameters (see text for estimation) of P and F_1 *Clethrionomys glareolus***

Reproductive parameter	N	r	p
Number of litters	13	−0.25	NS
Weaned young	13	−0.23	NS
Litter size	8	−0.34	NS
Start of reproduction	8	−0.40	NS

The applicability of this interpretation was examined as regards litter sizes and weight at weaning (Table 3). Litter sizes were significantly larger in the wild-caught (P) than in the laboratory-bred (F_1) females while female young at weaning (20 days) were heavier, although not significantly so, in the litters of F_1 females. However, a significantly lower

Table 3. **Litter size and female weaning weight in litters produced by P and F_1 *Clethrionomys glareolus* females, weighed before breeding started**

	Weight before breeding				Litter size				Weights of female young at weaning			
Mothers	N	$\bar{x}$	SD	Significance	N	$\bar{x}$	SD	Significance	N	$\bar{x}$	SD	Significance
P	40	18.5	2.1	$P<0.001$	141	4.9	1.2	$P<0.05$	219	9.1	1.9	NS
F_1	35	16.0	1.9		85	4.5	1.4		77	10.0	1.5	

weight had appeared at maturity in the F_1 females from P litters. Thus a negative effect due to alternating large and small litters was supported also by the present data. It is obviously due to limited body resources (energy or nutrients) and the mobilizable amounts of these resources are probably related to body size.

The correlations in Table 2 are not significant. However, the interpretation of them as maternal effects on reproduction is supported both by similar findings in two American small rodent species and by significant differences in a derived relationship between litter sizes and female weights. Thus, although the reproductive effects are not as evident as the correlations in body weight both may be used for evaluating ideas relating to weight and reproduction in free-living populations.

One of the correlates of the proposed mechanisms in the Chitty Hypothesis for cyclic vole populations, i.e. a strong heritability of male body weights, was thus observed also in a non-cyclic vole population, thereby indicating a lack of importance of this factor in population dynamics. The negative maternal effect may be important in the demography of cyclic populations if the cyclicity is caused by other factors. In the present study it was observed under the same nutritional conditions for parents and offspring. However, the body growth improved in animals taken into the laboratory from the field and given surplus food (Hansson 1985, unpubl.). In an increasing vole population there is more food per individual than in a peak population. Thus, the negative maternal effect should be much more obvious under field conditions in peak/decline populations. It may at least partly explain why increase-early peak animals reproduce early and have larger litters (Hansson and Henttonen 1985b) and why late peak-decline animals show low body weight and late start of breeding, as evident for *C. glareolus* in, e.g., Hansson (1984).

Summarizing, selective effects on individual characteristics related to body size do not cause vole cyclicity according to the Chitty Hypothesis while reproductive patterns in vole cycles, also appearing in the Chitty Hypothesis, may be explained by alternating positive and negative maternal effects.

Acknowledgements

I am grateful to Börje Larsson for genetical advice. The work was supported by the Swedish Natural Science Research Council.

Zusammenfassung

Korrelationen von Wachstum und Reproduktion zwischen Eltern und Jungtieren bei der Rötelmaus Clethrionomys glareolus in Beziehung zur Chitty Hypothese

An nicht zyklischen Populationenen von *Clethrionomys glareolus* wurden Korrelationen von Wachstum und Reproduktion zwischen Eltern und Jungtieren untersucht. Die Wechselbeziehungen in der Körpergröße waren positiv bei männlichen und negativ bei weiblichen Individuen. Die Wechselbeziehungen in bestimmten Fortpflanzungsparametern waren negativ und wurden weiter analysiert. Sie könnten durch einen negativen maternalen Effekt bedingt sein. Diese Befunde widersprechen der Chitty Hypothese zur Populationsregulierung, könnten aber die zyklischen Variationen von Gewicht und Reproduktion erklären, wenn äußere Faktoren die Zyklen beeinflussen.

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Z. Säugetierkunde 53 (1988) 11–21

ISSN 0044-3468

The swimming ability of *Ctenomys fulvus* (Ctenomyidae) and *Spalacopus cyanus* (Octodontidae), with reference to swimming in other subterranean mammals

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Receipt of Ms. 21. 5. 1986

Abstract

Investigated the capacity for swimming for the South American rodents, *Ctenomys fulvus* and *Spalacopus cyanus.* Like most non-cricetid and non-murid rodent moles which have been tested, both *Ctenomys* and *Spalacopus* were not strong swimmers (mean swim time <two minutes). *Spalacopus* showed flexibility within a strong stroking pattern, but its shaggy pelage was detrimental to floating, which is of primary importance to the swimming success of all subterranean mammals tested thus far. As a result of small body size (small body mass to surface area ratio is conductive to floating since the dense pelage traps air which increases buoyancy), insectivore moles have for the most part performed better during swimming trials than rodent moles; it is interesting to note that no aquatic or semi-aquatic rodent-moles have evolved to parallel the swimming ability of certain species of talpids, despite rodent moles having much greater taxonomic diversity at the family, generic, and specific levels. Studies on the distribution and swimming ability of non-vagile subterranean mammals have thus far concerned the ability to disperse by swimming and climbing, the influence of water on burrow structure, geographic variation in behavioural patterns associated with the amount of free standing water, establishment of a more complete ethogram of the behavioural repertoire of subsurface animals, morphological factors influencing swimming ability, the evolution of fossoriality from an aquatic origin, and adaptive radiation into aquatic niches. Zoogeographic analysis of subterranean forms should consider swimming ability as an integral part of the factors responsible for current patterns of distribution.

Introduction

The swimming of tuco-tucos (*Ctenomys,* Ctenomyidae: Rodentia) and coruros (*Spalocopus,* Octodontidae: Rodentia) is of interest in several respects: firstly, ctenomyids are one of the few subterranean mammals which transport excavated soil with the hind feet (Hickman 1985), a behavioural trait which could have important implications as to the manner and ability of swimming; secondly, the swimming ability of South American small mammals is virtually unknown (disregarding domesticated species such as guinea pigs *Cavia porcellus*), as is the swimming ability of most small mammals (Getz 1967; Wilber and Weidenbacher 1961; Dagg and Windsor 1972; Esher et al. 1978; Harris and Peterson 1979), so that chance or casual observations (Fredrickson 1972; Stock 1972) are noteworthy as representing the only knowledge available for an entire genera or even families; finally, ctenomyids are the only major group of non-cricetid and non-murid subterranean eutherian mammals (see Nevo 1979 for an overview of subterranean mammal types) which have not been tested for swimming ability. With one of the last pieces of the puzzle in position, a number of trends should become apparent in the manner and ability of swimming; these general trends are discussed with comments on the significance of swimming ability to the biology of subterranean mammals as a group.

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Materials and methods

One adult male (210 g) and adult female (314 g) *Ctenomys fulvus* were captured from San Pedro de Atcama, Region II, Chile, in September 1982. One subadult (65 g) *Spalacopus cyanus* was captured from Con Con Alto, Region V, Chile, in October 1982, and one adult male *S. cyanus* (190 g) was taken from Lagunillas, Region Metropolitana, Chile, in September 1982. Animals were air-freighted to South Africa where laboratory studies were undertaken.

Methodology followed the guidelines established for previous studies on the swimming ability of subterranean mammals (Hickman 1977, 1978, 1983; Hickman et al. 1983), permitting comparison with tests on swimming conducted under similar conditions.

Animals awaiting testing were housed separately in 31 cm wide, 92 cm long and 18 cm high all-glass terraria half-filled with sandy soil, at a temperature of 23 °C. A 50 cm wide, 122 cm long and 43 cm high all-glass aquarium was filled to a height of 23 cm with water at 23 °C. Animals were tested singly to obtain maximum performance (Wilber 1959, 1963; Wilber and Hunn 1960) between 8:00 h and 18:00 h, one trial per animal per day, three trials each, and the manner of swimming, speed, and endurance noted (documentation was by 35 mm photographs). Animals were removed from the water when it appeared as though the animals were in danger of drowning (about to sink without being able to resurface). Water was totally replaced for each trial to nullify any detergent effect urine might have on the air-trapping capacity of the pelage.

Following testing, animals were returned to their respective cages, where subsequent behaviour was noted.

Results

Ctenomys fulvus (mean 25.5 s) did not swim as well as *Spalacopus cyanus* (mean 85 s); no mortalities were incurred for either species.

Ctenomys fulvus

The 210 g male swam for 20, 15, and 30 s in progressive tests, while the 314 g female swam for 25, 20, and 55 s.

Twice during trials, the 210 g animal became totally immobile ("froze") when brought into contact with the water (a reaction to danger typical of many rodents), resulting in sinking without any effort to reach the surface. Even when stroking with the limbs occurred, splashing was never observed.

Swimming posture was horizontal (Fig. 1) with the eyes remaining open throughout the trials; however, the fur wetted rapidly, with the hindquarters gradually sinking until the tip of the snout was the last area to become submersed.

Propulsion by dog-paddle stroking did not involve sculling motions of the tail. The greatly enlarged hindfeet did not appear to hinder stroking, attaining maximum speeds of 30 cm/s. Turning involved little apparent effort.

Animals made no attempt at digging when returned to the cages after testing, but instead sat quietly on their haunches while grooming.

Spalacopus cyanus

The 65 g male swam for 45 and 165 s in progressive tests, while the 190 g male swam for 60, 25 and 25 s.

Stroking by *Spalacopus* commenced immediately upon contact with the water, without any splashing throughout the trials.

Body posture during swimming was at a slight angle to the surface (Fig. 2); nonetheless, the eyes positioned high on the head, normally useful when peering out of burrows, were kept well above the water while remaining open throughout the trials. The shaggy fur wetted quickly which required vigorous stroking for the animal to remain afloat.

The dog-paddle typical of many mammals was not supported by sculling of the tail (the short tail appeared highly tactile and was more useful as a probe rather than for

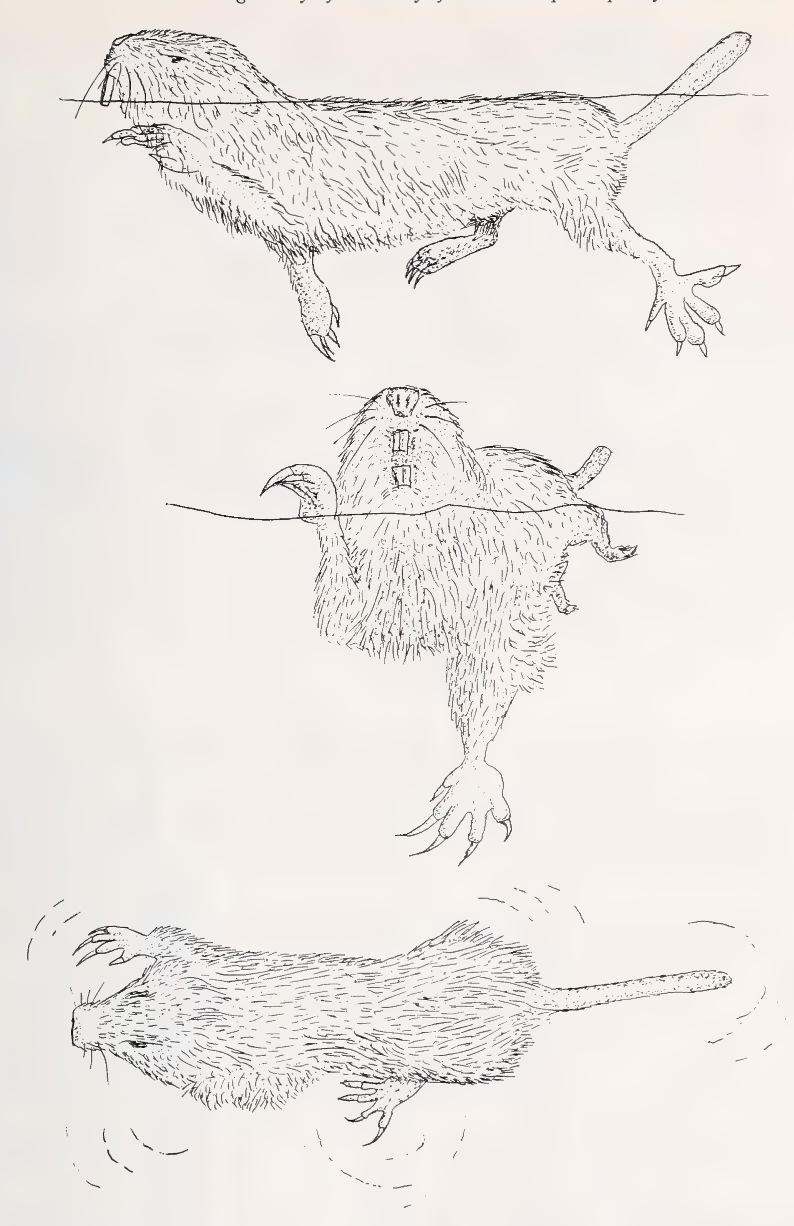


Fig. 1. Various views of *Ctenomys fulvus* swimming in an aquarium at 23 °C (drawn from photographs). *Above:* Side-view: note the horizontal body posture with snowshoe-like hindfeet; both fore and hindfeet with coordinated movements of the robust, tactile, tail (seen here partially lifted above the water) are also important in the transport of excavated soil. *Middle:* Three-quarter front view: the large foreclaws did not obstruct stroking, and the head with typically enlarged rodent incisors is maintained well above water level. *Below:* Top-view: only slight lateral movements of the hindquarters were noted; the tail was not used for sculling



Fig. 2. Side view of *Spalacopus cyanus* during an aquarium trial at 23 °C (drawn from a photograph); note that the hindquarters remained low in the water, despite hindfeet positioning close to the body and strong stroking provided by all four limbs

propulsion); the dog-paddle switched to synchronous hindleg kicking when swimming rapidly in linear paths, although the forelimbs continued to stroke alternately. *Spalacopus* paddled strongly, so that it is surprising that the hindquarters remained low in the water during swimming. Swimming speed reached a maximum of 30 cm/s, with turns being executed with little apparent difficulty.

No attempts at digging were made by animals when returned to the cages; animals either rested quietly or groomed themselves.

Discussion

Adaptations of marine mammals to swimming has been well documented for some time (Howell 1930), while the swimming of most terrestrial mammals has remained almost totally unrecorded (Dagg and Windsor 1972). Except for some early observations on talpids (Fisher 1885; Merriam 1884; Foot 1941; Reed and Rhiney 1943), the swimming ability of all subterranean mammals was unknown until recently (see Table), despite the

Table. **Classification of subterranean mammals tested for swimming ability, habitats sampled, projected width (m × min) of traversable water barriers, and sources of data**

Order	Family	Gernera tested	Capture site	Projected distance (m)	References
Insectivora	Talpidae	*Condylura*	Lake shore	1440	Hickman 1984b
		Parascalops	Lake shore	1080	
		Scalopus	Meadow	150	
	Chrysochloridae	*Amblysomus*	Grassland	360	Hickman 1986
		Eremitalpa	Desert	<1	
		Chrysospalax	Forest	8	
Rodentia	Geomyidae	*Thomomys*	Mountains	84	Hickman 1977
		Geomys	Plains	26	
		Pappogeomys	Plains	18	
	Bathyergidae	*Heterocephalus*	Semi-desert	54	Hickman 1983b
		Cryptomys	Grassland	35	Hickman 1978
	Rhizomyidae	*Tachyoryctes*	Grass, few trees	40	Hickman 1983a
	Octodontidae	*Spalacopus*	Mountains	38	Present study
	Ctenomyidae	*Ctenomys*	Semi-desert	9	Present study
	Spalacidae	*Spalax*	Mountains, desert	1	Hickman et al. 1983

fact that moles and mole-rats are generally very poor climbers (HICKMAN 1982) and are thereby committed to swimming should water rise to sufficient levels. Flat areas, and highways (HUEY 1941), and rivers (KENNERLY 1963; SMITH and PATTON 1980) are moist areas which form corridors for dispersal, and are habitats particularly vulnerable to flooding. Normally non-vagile due to the high energy costs associated with excavating burrows (VLECK 1979), subterranean mammals may thus be induced to disperse from established areas and facilitate gene flow as animals "hurdle" edaphic barriers while swimming. Moreover, colonization is facilitated as re-establishment of burrows is not excessively difficult in moist and friable soils upon reaching the shoreline. The above scenario must however, meet one very important basic requirement: the animals must be able to swim. Rafting does not appear to be of much consequence, since subterranean mammals made no attempt at clinging to or climbing on buoyant debris provided during some of the testing.

The swimming ability of *Ctenomys fulvus*, representing one of the last major eutherian families of subterranean mammals to be tested (Table), reinforces the general pattern which has emerged from previous studies: insectivore moles are, as a general rule, better swimmers than rodent-moles (Fig. 3). For those species tested, the mean swimming time for insectivore moles was 20 min to only three minutes for rodent moles and swimming rate 21 m/min to 12 m/min in favour of insectivore moles, resulting in a projected (m × min) overall advantage in dispersal distance of 608 m to only 34 m to the advantage of insectivore moles. The above figures are likely minimal, as favourable currents and larger sample sizes over many years would undoubtedly reveal greater dispersal powers. None-

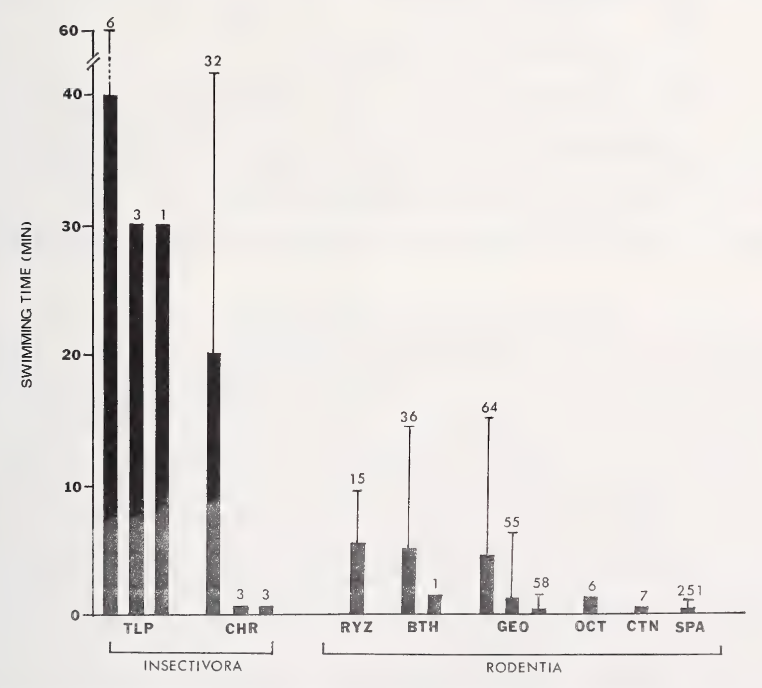


Fig. 3. Mean swimming times recorded for several species belonging to the major groups of eutherian subterranean mammals under laboratory conditions are indicated by bars; lines atop bars indicate the upper ranges during trials; the number of trials are given at the top of each line. TLP = Talpidae; CHR = Chrysochloridae; RYZ = Rhizomyidae; BTH = Bathyergidae; GEO = Geomyidae; OCT = Octodontidae; CTN = Ctenomyidae; SPA = Spalacidae. References for data and species for each column are listed in the Table

theless, laboratory testing has indicated an ability to traverse at least small waterways which may form an effective barrier to even surface rodents (SAVAGE 1973).

Insectivore vs Rodent moles

Size and pelage appear to be primarily responsible for the dichotomy in swimming performance between insectivore and rodent moles. The smaller size and weight of insectivore moles (a mean of 100 g to 146 g for rodent moles tested, see Fig. 4) results in a

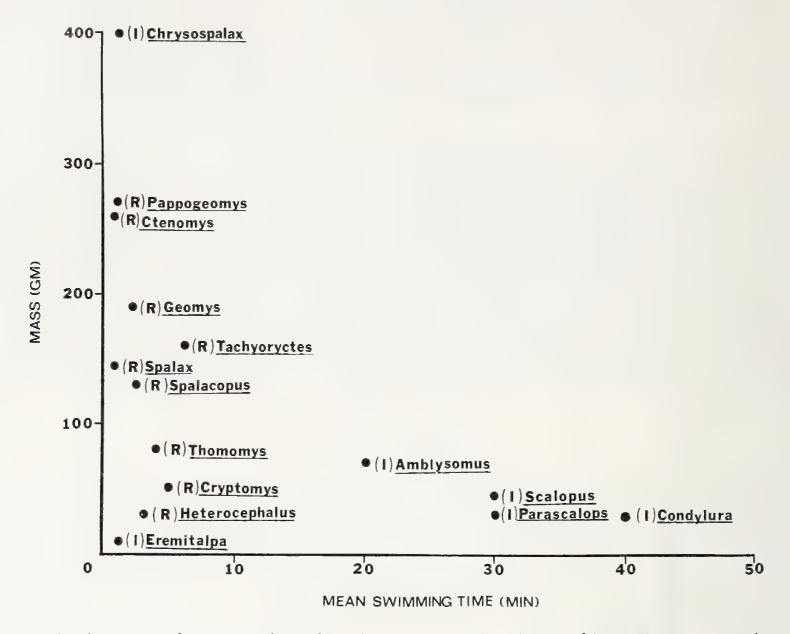


Fig. 4. Mean body mass of species plotted against mean swim times of insectivore (I) and rodent (R) moles

small body mass to surface ratio, with air trapped in the pelage exerting a greater influence on the buoyancy of swimming animals; the fur of talpids (the most successful subterranean mammal swimmers tested thus far) is renowned for thickness and insulative properties which not only assists floating, but protects talpids (which are small in size) from rapid temperature loss to the water. The uncharacteristic poor performance by an insectivore mole, the giant mole *Chrysospalax,* was largely attributable to the inability of these large animals to float (HICKMAN 1986), while the smallest of the rodent-moles tested *(Heterocephalus)* did not perform well due to the lack of fur and subsequent lack of floating ability (HICKMAN 1983b). None of the rodent-moles were able to float effectively due to the large skull and massive head musculature important to digging and gnawing vegetation; insectivore moles do not dig with the head and have lighter skulls with only moderately developed jaw musculature for crushing insects and severing earthworms. Moreover, talpids have an elongate snorkle-like snout which enables the nostrils to be held high above the water surface (HICKMAN 1984b). Other non-subterranean rodent species such as the fossorial muskrat *Ondatra zibethica* are good swimmers despite a large size (WILBER 1958, 1963), so that factors other than size and pelage must also contribute to swimming success for mammals in general.

Anatomical features other than size and pelage appear of less importance to the swimming ability of subterranean mammals. Although insectivore moles (the best

swimmers) are more characteristically blind than rodent moles, the only rodent-mole with eyes completely covered with skin *(Spalax)* was one of the worst of all mammal swimmers; all subterranean mammals, whether effective swimmers or not, maintained equilibrium when swimming. The more prominent mystacial vibrissae of rodent moles, important to other species of rodents during swimming (AHL 1982), appeared only minimally to assist with balance. The "comb" fringing the lateral edge of the foot of *Ctenomys fulvus* did not play a significant role for propulsion or balance.

Although the best swimmers (the talpids) were tailed, the next best swimming group (the chrysochlorids) lack any form of external tail; and although the worst rodent-mole swimmer *(Spalax)* lacks an external tail, the best rodent-mole swimmers *(Cryptomys)* have only a short, stubby tail. The tail is of some assistance as a probe and for maintaining balance in some moletypes not only during digging (HICKMAN 1984c) but also during swimming (BEST and HART 1976; HICKMAN 1979); the tail was utilized for propulsion when swimming only by *Condylura,* and then only during diving (*Condylura* was the only species tested which attempted diving).

The development of enlarged foreclaws for digging had little effect on swimming (geomyids vs bathyergids, for example), but the partial webbing of the digits common to many subterranean mammals (responsible for the misnomer *Scalopus aquaticus,* a non-aquatic species), normally utilized when pushing soil, appeared to contribute to effective stroking in the water (HANAWALT 1922). Other preadaptations to swimming common to both insectivore and rodent moles include a streamlined body contour, strong nasal sphincters, ability to withstand low oxygen levels, and powerful limb musculature.

The fact that *Ctenomys* differs from most subterranean mammals by transporting excavated soil to the surface by kicking with the back legs rather than turning around and pushing the soil with the anterior portion of the body (HICKMAN 1985) had no discernable effect on either the manner or ability to swim. In fact, most behavioural differences had little influence on swimming ability. A few insectivore and rodent moles remained motionless and floated instead of trying to swim, so that the fur wetted less quickly due to less water turbulence; however, immobile animals would stand little chance of reaching the safety of the shore under natural conditions. *Spalax* was one species where a few individuals were able to improve on swimming performance by utilization of a characteristic "head lift" (HICKMAN et al. 1983).

Predicting swimming ability

With convergent anatomical adaptations and little behavioral differentiation in swimming behaviour, how predictable is a species performance in water? Two general trends emerge from studies on the swimming ability of subterranean mammals: 1. insectivore moles swim better than rodent-moles; 2. smaller species of mole types swim longer than larger mole types. There are, of course, exceptions to the trends; the large size of *Chrysospalax* for an insectivore mole is the exception to the first trend which substantiates the second trend. Yet, one of the few species of any mammal mole-type to adapt to an aquatic existence, the talpid *Desmana* (250–400 g), has an adaptation of many aquatic mammals: large size (relatively speaking) for low surface to body mass ratio which conserves heat and offers some degree of protection from predatory amphibians (PINE 1975), fish, or birds. On the other hand, the Pyrennean desman (*Galemys,* 50–80 g) retains the small size of most subterranean mammals, as has an aquatic insectivore shrew, *Neomys* (10–20 g). Surprisingly, although talpids include the aquatic *Desmana* and semi-aquatic *Condylura,* the other insectivore mole-group, the chrysochlorids, have not radiated into even the semi-aquatic habit (HICKMAN 1986), and the only reference found for any group of rodent-mole was for the ctenomyid *Ctenomys lewisi* (WALKER 1975 p. 1047) which, ". . . tunnels in stream banks and may be semi-aquatic". There is little to suggest in the present study on *C. fulvus*

or any other rodent-mole that any species of rodent-mole regularly visits water and swims, despite the promise of plentiful food resources, a means of escaping predators, and extensive energy savings (Vleck 1979) by circumventing the need for excavating extensive tunnel systems. No mole-type has widely colonized the marine littoral environment (McCulley 1967) although some species *(Bathyergus)* may be found in dunes. Since the subterranean environment is stable, reliable, and safe (most moles are K-selected), adaptive pressures would have to be very strong to promote abandonment of the sub-terrestrial niche and the risks involved with numerous novel situations.

Perhaps habitat differences between various mole types may give some indication of swimming ability. Subterranean mammals establish tunnel systems in a wide variety of habitats (Table), with insectivores more characteristically inhabiting moister areas where invertebrates are more numerous. Rodent-moles are also abundant in moist areas where there is an abundance of plants to eat, but are also found in drier areas less characteristic of insectivore moles where tubers, bulbs, and other geophytes are available. Insectivores from moist areas are much better swimmers, even swimming through water-filled tunnels (Moore 1939). Rodent-moles *(Spalax)* from mountainous areas with seasonal flooding are better swimmers than con-specifics from desert habitat (Hickman et al. 1983). Hickman (1977) also suggests that regular spring-flooding in mountainous areas would select for swimming adaptations in geomyids (*Thomomys* were the best geomyid swimmers tested); however, Bainter and Hart (1979) cite good drainage in mountainous areas as not selecting for swimming ability. In any event, much water is seasonally available in mountainous areas, and a potential influence on swimming ability. Habitat may affect body size, amount of fat deposits, development of musculature, oiliness of the pelage, and many other physical characteristics which might indirectly affect buoyancy and swimming; however, no systematic studies have been conducted to determine the effect of these factors, and predicting swimming ability remains tenuous at best.

Moreover, there is a need for wider experimentation with a wider range of mammalian types before further generalities can be formulated and the significance of the results appreciated. In comparison with some rodent species (Esher et al. 1978), insectivore moles compare quite favourably, yet other rodents such as *Microtus* swim at least as well as insectivorous moles (Carter and Merritt 1981; Fisher 1961), a characteristic which has enabled colonization of coastal islands.

The value of studies on swimming

Aside from practical value (evaluating flooding as a control measure for mole-types in agricultural or horticultural areas, as a test for the effectiveness of drugs (Shapiro et al. 1970), or as a water barrier for zoological gardens), there is heuristic value in having a comprehensive ethogram for mammals; many numerous and widely distributed animals (*Ctenomys,* for example, which extend almost the entire length of South America) have remained totally untested for swimming ability. Swimming ability, not as an end in itself but in conjunction with other factors, can be an important tool to zoogeographic analysis (Smith and Patton 1980; Wilkins 1985), enabling more knowledgeable interpretation of such behaviours such as position of the nest and direction of tunnel extension (Miller 1957; Williams 1976). Thus far, studies on the swimming ability of subterranean mammals have involved the importance of various morphological, behavioural and abiotic factors (Hickman 1978, 1982, 1983b) to swimming success; phylogenetic affinities by use of behaviour as a taxonomic tool (Hickman 1977); the question of an aquatic vs terrestrial origin for talpids (Hickman 1984a); examination of the question why subterranean mammals have not more widely radiated into aquatic niches (Hickman 1986); the ecology of seasonal flooding (Hickman 1983a); and the importance of water as a barrier to dispersal and subsequent speciation (Kennerly 1963; Hickman et al. 1983).

Concerning mammals as a group, areas of study such as the ontogeny of swimming ability remain largely unexplored (King 1961; Schapiro et al. 1970; Dagg and Windsor 1972), while further studies are needed to compare swimming performances within genera (Schmidley and Packard 1967; Hafner and Hafner 1975), within (Evans et al. 1978) or between (Hickman and Machine 1987) families, and even between orders (Starrett and Fisher 1970). Much further basic experimentation and understanding in terms of events which occur only rarely or remain for the most part unobserved is needed for a full appreciation and evaluation of free water as a significant feature in dispersal, adaptive radiation, and general biology of subterranean mammals, or indeed, of mammals in general.

Acknowledgements

In Chile, Dr. Mario Rosenmann and Sr. Rigoberto Solis of the Universidad de Chile were most helpful with equipment, advice, and translations. Luis Contreras kindly procured live tuco-tucos and coruros and arranged for safe shipment of the animals to South Africa; the C.S.I.R. made the study possible with a post-doctoral bursary and travel allowance, in conjunction with the University of Natal which provided a leave furlough with travel grant. Susie, my wife, wore the cap of secretary, mother, adviser, and not least of all, cheerleader, throughout the study. Gordon Maclean undertook the translation of English to German, and Julie Cook kindly transformed pages of scibble to legible text. The kind assistance of everyone during this and associated studies is gratefully remembered.

Zusammenfassung

Die Schwimmfähigkeit von Ctenomys fulvus (Ctenomyidae) und Spalacopus cyanus (Octodontidae) im Vergleich zu anderen subterranen Säugetieren

Die Schwimmfähigkeit von *Ctenomys fulvus* (Ctenomyidae) und *Spalacopus cyanus* (Octodontidae) wurde untersucht. Wie die meisten anderen bisher untersuchten, wühlenden Nager sind diese Arten mit durchschnittlich unter 2 min Schwimmzeit wenig ausdauernde Schwimmer. Hinderlich bei *Spalacopus* war offensichtlich sein schnell durchnässendes Fell.

Ein Vergleich der Schwimmfähigkeit bei wühlenden Nagern und Insektenfressern ergab: Wühlende Insektenfresser (untersucht wurden Talpidae und Chrysochloridae) sind im Durchschnitt bessere Schwimmer als wühlende Nager. Innerhalb der Gruppen wühlender Nager hat sich keine Art an das Wasserleben angepaßt, wie das die Desmaninae innerhalb der Talpidae getan haben.

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Z. Säugetierkunde 53 (1988) 22–30

ISSN 0044-3468

Wild boar social groupings and their seasonal changes in the Camargue, southern France

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Receipt of Ms. 29. 1. 1987

Abstract

Wild boar social organization and its monthly changes were studied from 872 sightings of groups, recorded in the Camargue (southern France) from December 1975 through February 1983. Groups, comprised of 1 to 23 animals, were classified according to their composition. There were three recognized age categories: piglets, subadults, and adults. Of the 872 groups, 240 (27.5 %) were single adults, 134 (15.4 %) consisted of adults grouped together and 119 (13.6 %) were subadults observed either singly or grouped together. The most frequent groups (N = 379, 43.5 %) were matriarchal units; they were generally comprised of 1 to 5 sows with their piglets and/or yearlings. The study of monthly variations in the percentage frequency observed for the various group categories showed that the social structure of wild boar is a dynamic system that changes throughout the year in relation to the farrowing and breeding seasons.

Introduction

Despite the large literature on wild pigs (Mauget et al. 1984), there is little information on their grouping patterns.

Group size and composition have been described in some studies dealing with the general ecology and behaviour of the species (Sludskii 1956; Snethlage 1957; Gundlach 1968; Eisenberg and Lockhardt 1972; Frädrich 1974; Beuerle 1975; Graves and Graves 1977; Barrett 1978; Shaffer 1979; Santiapillai and Chambers 1980; Singer and Ackerman 1981; Meynhardt 1982). Formation of family units appears characteristic of wild pigs. Their social organization has been described as a matriarchal society with the basic family group comprised of a sow and its young of the year. Multifamily groups, composed of several sows with their young have been termed "sounders" by Eisenberg and Lockhardt (1972). Extended family groups also include subadults which are presumably offspring of the previous year (Shaffer 1979). In contrast, adult males are solitary; they join females only during the breeding season.

Little attention has so far been paid to seasonal changes in grouping patterns and their determining factors. Sludskii (1956) or Santiapillai and Chambers (1980) have shown that various environmental factors such as temperature, snow cover or availability of food can cause changes in group size of wild pigs. In other respects, various results indicate that changes in social organization occur during rutting and farrowing time.

The present paper reports a study of group size and composition of wild boars living in the Camargue, and analyzes changes related to the farrowing and breeding seasons.

Study area

Sightings of wild boar groups have been recorded at the Tour du Valat Reserve, which is privately owned land with minimal human access. It covers an area of 1500 ha and is located in the southeastern part of the Rhône delta. Lying to the east of the Camargue National Reserve, the area is surrounded on its other sides either by cultivated land or by more or less natural ground.

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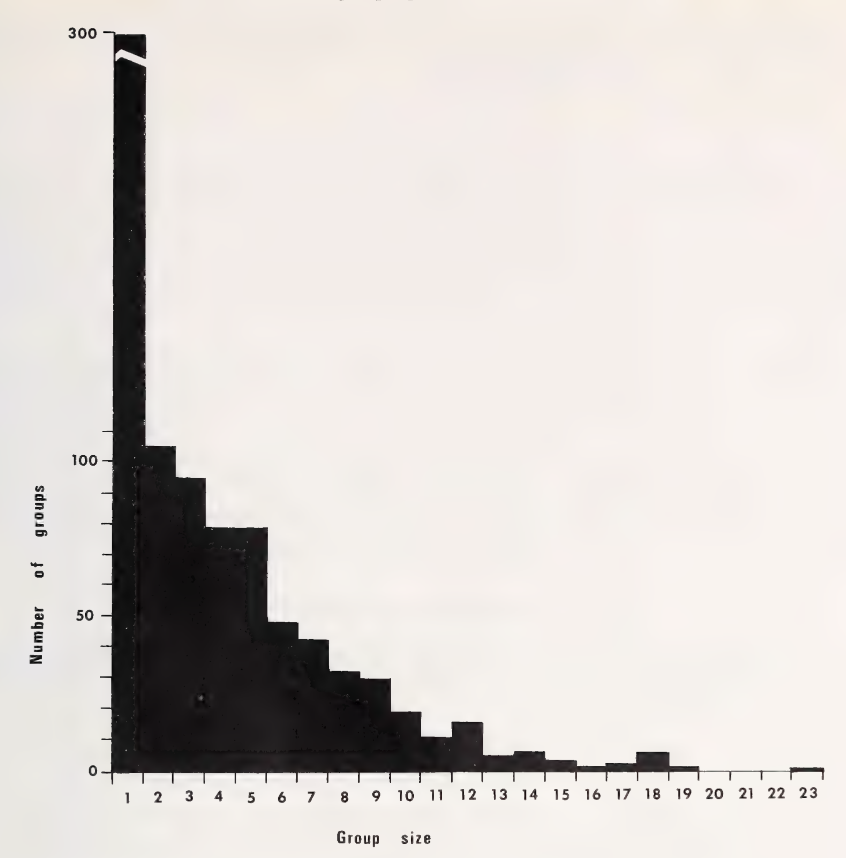


Fig. 1. Frequency diagram indicating the group size for the wild boar in the Camargue, southern France

Material and methods

Observations and sightings of wild boar groups were mainly made by game wardens and researchers of the "Tour du Valat Biological Station" during their regular field work. From December 1975 through February 1983, these observers noted the composition and location of the wild boar groups observed on pre-established tables and maps, which were fixed on a board in the hall of the research building.

The animals observed were classed in three age categories according both to their estimated weight and coat color. Piglets, i.e. young with a striped coat, were generally less than 4 months old and weighed less than 15–20 kg. Subadults had a reddish or black coat, and a weight varying from 15–20 to 30–40 kg. Adults referred to animals more than 2 years old; they looked big, heavy and dark or silver grey colored.

With a few exceptions, sex was not specified because it could not be reliably determined at a distance.

Results

A total of 3530 animals in 872 distinct sightings were observed during the 7 years of the study. Of the 3530 wild boars observed (fig. 1), 240 (8.2 %) were single adults, 59 (1.7 %) were single subadults or piglets, while 3241 (91.8 %) animals were encountered in 583 groups composed of 2 through 23 animals. The most frequent group sizes were 2 (18.0 %)

and 3 (16.3 %), then 4 and 5 (13.5 % each). Groups of more than 10 animals were seen only occasionally (12.3 % of the 583 groups).

Group categories

The 872 sightings ranged in the 11 following categories: 1. Single adults (n = 240, 27.6 %); 2. Adult-groups (n = 134, 15.4 %); 3. Single subadults (n = 41, 4.7 %); 4. Subadult-groups (n = 78, 8.9 %); 5. Groups of both adults and subadults (n = 281, 32.2 %); 6. Basic family group = 1 adult with piglets (n = 27, 3.1 %); 7. Sounders = several adults (2 to 5) with piglets (n = 36, 4.1 %); 8. Extended family groups = adults with both piglets and subadults (n = 16, 1.8 %); 9. Single piglets (n = 8, 1.0 %); 10. Piglet-groups (n = 9, 1.0 %); 11. Subadult- and piglet-groups (n = 2, 0.2 %).

Categories numbered 5 to 11 must all be considered as matriarchal in nature. Groups of adults with piglets include the categories "family groups" (n° 6) and "sounders" (n° 7), previously mentioned, whereas groups comprised of adults and subadults (n° 5) are supposedly a later stage of this type of association. Category n° 8 has previously been termed "extended family group". The 19 groups that make up the categories n° 9, 10 and 11 have to be included in matriarchal associations because they all had at least one piglet; we suppose that one or more sows were either absent or out of sight for the observer.

Monthly variation in average group size

The average group size was about 4 animals. It ranged from 3.3 to 3.7 from January to May. It exceeded the annual average from June through December, ranging from 4.2 in July to 5.2 in October (fig. 2).

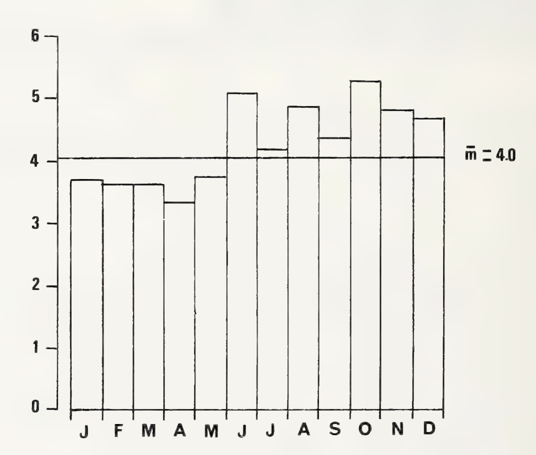


Fig. 2. Monthly variation in mean group size, in wild boars living in the Camargue, southern France

A more precise analysis has revealed that the proportion of groups formed of at least 4 animals increased from July through December, whereas that of groups including less than 3 animals decreased. The shift is observed only in August if the comparison takes into account groups of more than 5 animals and those of less than 4 animals. This means that wild boars regroup gradually during the summer and autumn seasons, and consequently live in larger groups during the second part of the year than during the first part.

Table. **Monthly changes in the relative frequency of the various wild boar group categories observed in the Camargue (southern France)**

n°	Group category	J	F	M	A	M	J	J	A	S	O	N	D	Total
1	Single adults	40	34	44	31	16	5	7	7	9	20	15	12	240
		33.9	29.0	31.7	29.8	27.6	23.8	24.1	18.0	20.4	24.4	21.4	23.5	27.5
2	Adult-groups	21	22	19	14	6	4	3	3	5	15	13	9	134
		17.8	18.8	13.7	13.5	10.3	19.0	10.3	7.7	11.3	18.3	18.6	17.7	15.4
3	Single subadults	6	6	3	13	2	0	2	3	1	3	2	0	41
		5.1	5.1	2.2	12.5	3.5	–	7.0	7.7	2.3	3.7	2.9	–	4.7
4	Subadult-groups	9	7	14	14	9	3	2	1	4	5	5	5	78
		7.6	6.0	10.1	13.5	15.5	14.3	7.0	2.6	9.1	6.1	7.1	9.8	8.9
5	Adults with subadults	38	44	54	10	1	1	4	18	20	36	33	22	281
		32.2	37.6	38.8	9.6	1.7	4.8	13.7	46.1	45.4	43.9	47.1	43.1	32.2
6	Basic family groups	1	1	1	9	5	0	5	0	1	1	0	3	27
		0.9	0.9	0.7	8.7	8.6	–	17.2	–	2.3	1.2	–	5.9	3.1
7	Sounders	3	2	2	9	10	3	3	2	0	0	2	0	36
		2.5	1.7	1.4	8.7	17.3	14.3	10.3	5.1	–	–	2.9	–	4.1
8	Extended family groups	0	1	1	2	3	4	2	0	1	2	0	0	16
		–	0.9	0.7	1.9	5.2	19.0	7.0	–	2.3	2.4	–	–	1.8
9	Single piglets	0	0	1	0	1	1	1	3	1	0	0	0	8
		–	–	0.7	–	1.7	4.8	3.4	7.7	2.3	–	–	–	0.9
10	Piglet-groups	0	0	0	2	4	0	0	2	1	0	0	0	9
		–	–	–	1.9	6.9	–	–	5.1	2.3	–	–	–	1.0
11	Subadults with piglets	0	0	0	0	1	0	0	0	1	0	0	0	2
		–	–	–	–	1.7	–	–	–	2.3	–	–	–	0.3
	Subtotal categories 6 to 11	4	4	5	22	24	8	11	7	5	3	2	3	98
		3.4	3.5	3.5	21.2	41.4	38.1	37.9	17.9	11.5	3.6	2.9	5.9	11.2
	Total	118	117	139	104	58	21	29	39	44	82	70	51	872

Monthly changes in group composition

Changes concerning groups with piglets

98 groups – categories n° 6 to 11 – included at least one piglet (table). Their percentage frequency greatly increased in April (fig. 3) and reached its maximum in May (41.4 %, table) when most females had given birth; at that time piglets follow their dam and were thus more easily sighted.

Piglets were seen alone in 11.1 %, 16.3 % and 58.3 % of the observations in March-April, May through June and August-September, respectively. This result indicates that as they increase in age piglets spend relatively less time in the close vicinity of their dam.

Groups including piglets became rarer in August, then again in September when piglets changed their coat color and were therefore identified as subadults by the observers (fig. 3).

From October through March, the monthly frequency was low and more or less constant. A basic level, less than 5–6 % (table), was registered during this period, which means some births occurred every month.

The maximal percentage frequency of basic family groups was observed in April and May (fig. 4^F), whereas that of sounders and extended family groups was reached in May for the first category (fig. 4^G) and in June for the second (fig. 4^H).

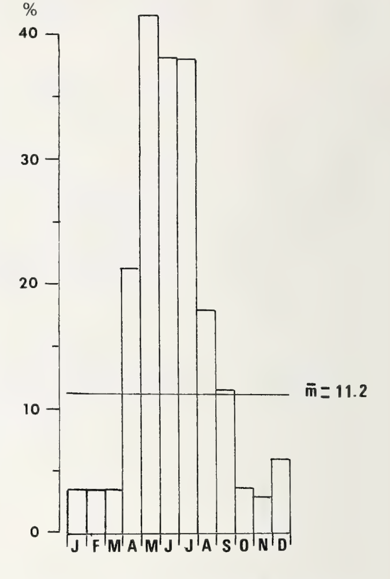
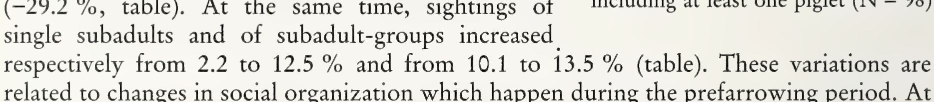


Fig. 3. Monthly variation in the relative frequency of wild boar groups including at least one piglet (N = 98)

Changes concerning subadults

The percentage frequency of groups comprised of both adults and subadults greatly diminished in April (−29.2 %, table). At the same time, sightings of single subadults and of subadult-groups increased respectively from 2.2 to 12.5 % and from 10.1 to 13.5 % (table). These variations are related to changes in social organization which happen during the prefarrowing period. At that time, sows become separated from their congeners and thus from subadults.



Single subadults were most frequently observed in April (fig. 4^D). They certainly regrouped during the following weeks as indicated by comparison of figures 4^D and 4^E. We can thus observe that the percentage frequency of single subadults diminished in May and June, whereas that of subadult-groups became higher than in April.

Groups comprised of females with both piglets and subadults were formed again during May through July (fig. 4^H). We therefore observed that the frequency of subadult-groups clearly decreased from May through August (fig. 4^E) whereas groups of adults with subadults (fig. 4^C) increased by 44.4 %. The increase was particularly high (+32.4 %, table) between July and August because piglets, which had lost their stripes, were subsequently identified as subadults by the observers.

Changes concerning adults

Sightings of adults observed either alone or grouped together (fig. $4^{A,B}$) decreased progressively from April through August (respectively −11.8 % and −5.8%, table), on

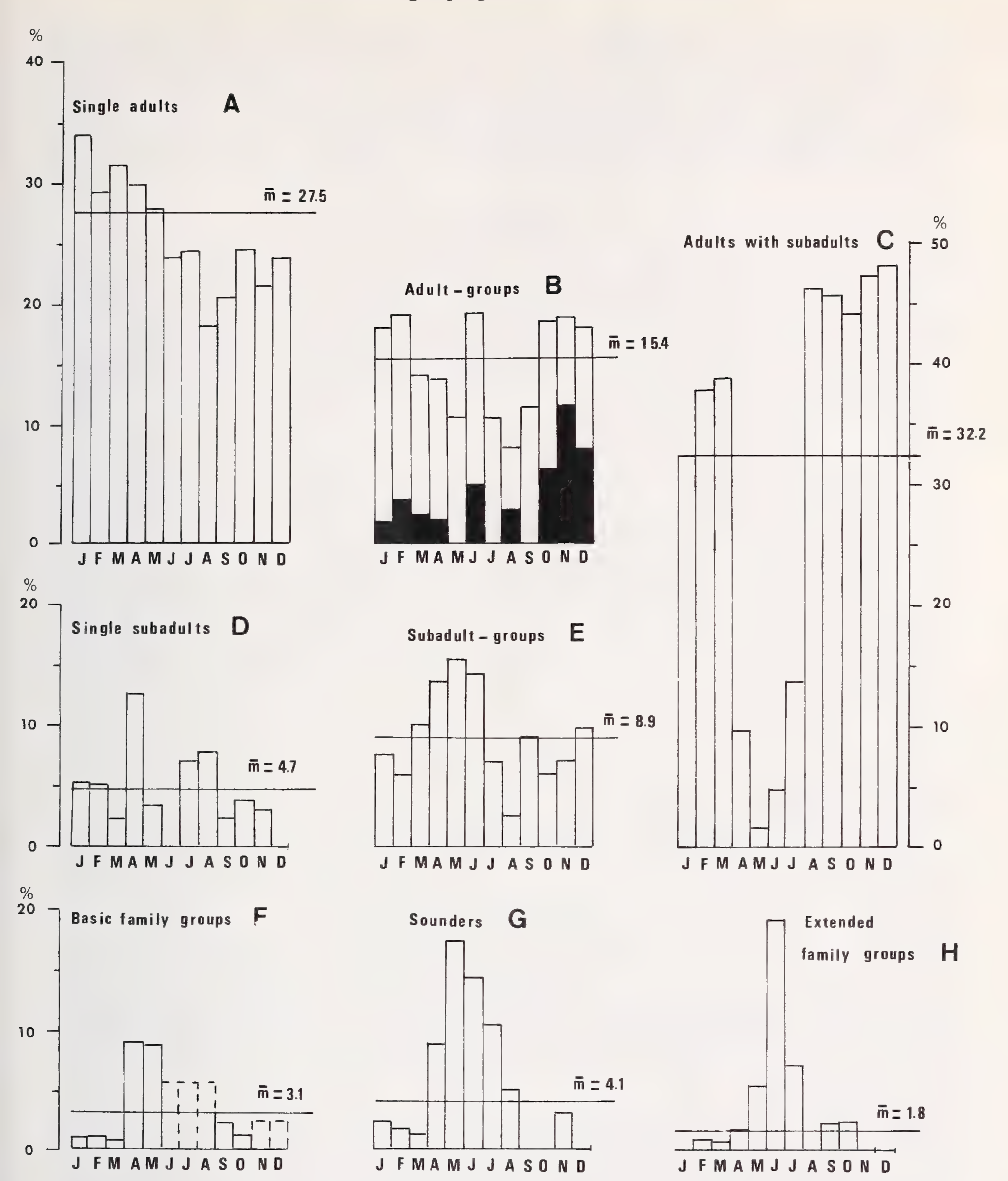


Fig. 4. Monthly variation in the relative frequency of the various group categories, in wild boars living in the Camargue, southern France. In the fig. 4^{B} black parts indicate relative frequency for adult-groups comprised of at least 5 animals

account first of the birth of piglets then of the reformation of extended family groups. From August through March, adults were encountered mainly in the company of subadults (table). However, adult-groups were rather frequent from October through February (fig. 4^{B}). Adults appeared to regroup in September (+3.6 %) then in October (+7.0 %). The percentage frequency of groups including at least 5 adults was clearly above the average annual percentage from October through December (fig. 4^{B}). This regrouping

of adults was related to the onset of the breeding season which was at its peak in early December. Afterwards, some adults, especially male wild boars, became solitary again as attested by the increase (+10.4 %, table) in the percentage frequency of single adults in January (fig. 4[A]). At that time, adult-groups remained rather frequent (fig. 4[B]), but they were smaller than observed during the prerut and rut seasons.

Discussion

Wild boars living in the Camargue exhibit the same basic social organization as has been previously described in other areas. Adults live either singly or in groups almost always including juveniles (subadults and/or piglets). According to the literature and our own observations of marked individuals (unpublished data), we think that single wild boars are mainly males whereas those living in groups are sows. When not in the company of adults, subadults are encountered either alone or grouped together.

Our results show that the social structure of wild boar is a dynamic system that changes throughout the year in relation to the farrowing and breeding seasons. At farrowing time, i.e. mainly in April, matriarchal groups are disrupted when gestating sows become isolated some days before they give birth. Meynhardt (1982) observed a 4-year female at farrowing time and reported that the female was followed by its young of the previous year when separating from congeners; afterwards, young remained with their mother which kept them at a distance of at least 20 m during nest building, farrowing and the post-partum period. However, the separation from congeners seems to be the rule in most other areas (Snethlage 1957; Gundlach 1968; Frädrich 1974). In addition, a number of radiotracking studies have shown that sows reduce their movements and tend to center their activities around nests before farrowing (Kurz and Marchinton 1972; Barrett 1978; Mauget 1980; Douaud 1983; Janeau and Spitz 1984). Consequently, subadults remain alone or grouped in small units. Results obtained in the Camargue show that single subadults would soon attempt to find companions.

After a postpartum seclusion period (Kurz and Marchinton 1972; Mauget 1980; Singer et al. 1981), piglets leave the farrowing nest and follow their mother. The family group, comprised of the sow with its piglets, may thereafter grow larger by association with other animals as has been observed by Snethlage (1957), Gundlach (1968), Mauget (1980) or in the present study. Our results show that sounders – which result from the joining up of at least two family groups – are chronologically the first type of association. The good synchronization of births observed in the Camargue would facilitate their formation since piglets are of similar age and development. In other areas, sounders have been observed to form during the first two weeks after birth (Snethlage 1957; Meynhardt 1982).

Sounders are the equivalent of nursery groups reported in other species of Ungulates such as caribou (Pruitt 1960), bighorn sheep (Geist 1971) or reindeer (Helle 1981). However, these groups seem to be smaller in wild pigs, although large sounder associations have sometimes has been observed by several authors (Snethlage 1957; Meynhardt 1982; other references in Singer and Ackerman 1981).

Extended family groups are formed from May through June. As observed in bighorn sheep (Geist 1971), it seems that reassociations with yearlings occur only 3–4 weeks after young are born. For Snethlage (1957), the spring separation from the mother is definitive. If some yearlings rejoin sounders in August, i.e. 4–5 months after births, most of them remain together and form large subadult-groups ("companies"). For his part, Meynhardt (1982) observed that the animals of the same matriarchal unit regroup only a few days after farrowing. In this case, the separation of group members is both more limited (see above) and more temporary than observed in the Camargue.

Strong bonds exist between family members and especially between closely related females (mother-daughter, sisters . . .) which would preferentially reassociate after the farrowing seclusion. Frädrich (1974) indicates that young females live with their mother until they reach sexual maturity. However, even if it lasts only a short time, the disassociation is certainly favourable to the dispersal of yearling females. They may follow some older female and thus switch to another matriarchal group if they happen to meet one.

With regard to the disassociation of yearlings from their mother during the rutting season, results obtained by various authors are also quite different. Most authors state that yearling males are chased away by adult boars (Nasimovich 1966 in Frädrich 1974; Beuerle 1975; Santiapillai and Chambers 1980). With respect to 2 years old males, which reach their sexual maturity at that time, Snethlage (1957) indicates that they leave the group voluntarily. For Gundlach (1968), female yearlings are also chased away by boars. This author states that both male and female yearlings rejoin their mother after rut. For his part, Beuerle (1975) thinks that the disassociation of yearling males is definitive; they would live in subadult-groups, then become solitary.

In the Camargue, wild boars are more gregarious from June through December than during the first part of the year. The groups grow larger firstly on account of the formation of sounders and extended family groups, then, during the prerut and rut periods, because of boars joining matriarchal groups to breed. The prerut period is characterized by an increase of adult-groups including at least 5 animals, from October through December. This prerut period would also exist in other populations of wild pigs. For example, Pfeffer (1961) indicates that Sludskii (1956) observed fighting between adult boars from August while in Central Asia breeding activities occur later on, in November and December.

Acknowledgements

The research was supported by the Foundation Tour du Valat. I am grateful to all people who have placed their observations of wild boars at my disposal. I wish to thank Prof. R. Campan for his advice and guidance during the course of the study, J. Smith and R. Cooke for correcting the English translation, and Y. Meyer for providing the German version of the summary.

Zusammenfassung

Soziale Gruppenbildungen und ihre jahreszeitlichen Änderungen bei Wildschweinen in der Camargue, Südfrankreich

872 Gruppen von Wildschweinen, die zwischen 1 und 23 Individuen enthielten, konnten in der Camargue beobachtet werden. Sie wurden aufgrund ihrer Altersverteilung klassifiziert. 240 (27,5 %) der beobachteten Gruppen bestanden aus einzelnen Adulten, 134 (15,4 %) enthielten mehrere Individuen, jedoch nur Erwachsene, und 119 (13,6 %) waren entweder einzelne Jungtiere oder Jungtiergruppen. Die häufigste Gruppenbildung (379, 43,5 %) stellten Mutterverbände dar. Sie bestanden aus 1 bis 5 Bachen, die mehrere Frischlinge und/oder Jungtiere führten. Die Analyse der monatlichen Änderungen in der Häufigkeit der verschiedenen Gruppen zeigt, daß die soziale Struktur bei Wildschweinen ein dynamisches System ist, dessen Änderungen im Laufe des Jahres mit der Paarungszeit und der Geburtszeit korreliert sind.

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Z. Säugetierkunde 53 (1988) 31–47

ISSN 0044-3468

Variabilité comportementale à l'intérieur du genre *Cephalophus* (Ruminantia, Bovidae), par l'exemple de *C. rufilatus* Gray, 1846

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Reception du Ms. 27. 10. 1986

Abstract

Behavioural differences in the genus Cephalophus (Ruminantia, Bovidae), as illustrated by C. rufilatus Gray, 1846

Studied the behaviour of *Cephalophus rufilatus* in captivity. Although most behavioural characters are shared by other duikers, this species shows some unique features as yet not encountered in the genus *Cephalophus:* lack of social play and reciprocal allogrooming, Laufschlag very rudimentary, mount of partners by the receptive female, droppings in pile, etc. ... *C. rufilatus* is intermediate between diurnal and nocturnal species, according to specific behaviour as well as social life. The genus *Cephalophus* is very homogeneous in basic behaviours such as locomotion, excretion, marking and reproduction, but variable, considering behavioural patterns directly depending on life conditions (habitat, diet and activity rhythm). Accordingly, due to actual presence of "archaic" and "advanced" characters, the duiker group cannot any longer be considered as the most primitive among Bovids.

Introduction

L'étude de la biologie des Céphalophes connait actuellement un certain développement, et ceci correspond sans doute au fait que cette sous-famille de Bovidés est morphologiquement l'une des plus homogènes, qu'elle est abondamment représentée dans toutes les formations forestières d'Afrique, et que son étude était restée jusqu'à présent à peu près totalement négligée. Faute d'arguments paléontologiques, on ne connait rien de l'origine de ce groupe original, de ses rapports avec les autres Bovidés et il est donc difficile de lui assigner un niveau phylogénétique et évolutif précis.

Dans la plupart des ouvrages, les Céphalophes sont habituellement présentés selon un modèle unique de petit ruminant forestier, crépusculaire ou nocturne, et solitaire. Cela reflète l'extrême indigence des renseignements dont on dispose sur eux, mais cela représente également une caricature de la réalité, puisqu'il existe, au contraire, de grandes différences interspécifiques: – dans la taille et le poids corporel (3 à 80 kg); – dans la morphologie (espèces pourvues de cornes dans les 2 sexes ou, au contraire, cornes présentes uniquement chez les mâles; corps lourd et trapu, monté sur des pattes courtes, ou léger avec de longs membres); – dans l'écologie (hôtes de pleine forêt, de régions arbustives ou même de steppes; espèces de terrain sec ou espèces localisées au bord des cours d'eau); – dans l'alimentation (frugivores ou folivore-herbivores); – dans le rythme d'activité (diurnes ou nocturnes exclusifs, ou diurne-nocturnes); – dans le comportement et la vie sociale (solitaires ou couples stables; contacts interindividuels rares ou très fréquents et variés).

Une espèce, *Cephalophus rufilatus* Gray 1846, semble occuper une place particulière, puisqu'elle présente un certain nombre de traits permettant de relier les nombreuses espèces de pleine forêt du genre *Cephalophus* au genre monospécifique de savane et de steppe *Sylvicapra.* Comme la plupart des autres espèces de Céphalophes, on peut estimer que sa biologie est inconnue, puisque seul Dittrich (1972) en a fait une brève étude en

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captivité. Par comparaison avec les quelques espèces sur lesquelles nous avons quelques renseignements précis, il semble donc nécessaire de dresser un premier bilan de son comportement, de manière à pouvoir mieux comprendre le groupe des Céphalophes par comparaison avec les autres Bovidés.

C. rufilatus se rencontre au nord de l'Equateur, de la Gambie jusqu'à l'ouest de l'Ouganda. C'est un habitant des forêts claires, galeries forestières ou bordures de forêt, parfois même de la savane, mais jamais de la forêt ombrophile dense. C'est une espèce d'assez petite taille, de 10 à 14 kg (Blancou 1958, 1962; Haltenorth 1963; Kingdon 1979, 1982; Ralls 1984). Le corps est légèrement bas du devant, de couleur rouge-orangée avec une teinte gris-noir sur le museau et le front, le milieu de la croupe, la queue et les pattes. Il n'y a pas de plages blanches bien nettes, si ce n'est un peu sur la lèvre supérieure et le bord des oreilles. La touffe frontale est développée dans les deux sexes. Les glandes préorbitaires, proéminentes, s'ouvrent selon une ligne rectiligne de pores. L'espèce est pourvue de glandes inguinales. Le mâle seul possède des cornes, la femelle ne présentant que des petits boutons osseux plus ou moins invisibles à l'extérieur. On ne connait ni son rythme d'activité ni son régime alimentaire: elle pourrait être diurne-nocturne et se nourrir de fruits, feuilles et herbes (Baudenon 1958; Haltenorth 1963; Kingdon 1982). Dans la nature, on rencontre les animaux le plus souvent seuls, rarement à 2 ou 3.

Matériel et méthodes

Les observations ont été faites au Zoo de Piétat (France) en septembre 1982 et juin 1983. Les animaux avaient à leur disposition un terrain d'environ 7.000 m^2, comprenant une prairie centrale de 2.800 m^2, parsemée de quelques arbres et bordée par une zone partiellement boisée comprenant différents abris.

L'espèce y a été introduite en 1974. Depuis cette date, des naissances ont eu lieu régulièrement chaque année. Au début de notre étude, la population comptait 6 individus: un mâle adulte de 6 ans (M1), 2 femelles adultes de plus de 7 ans (F1 et F2), une femelle subadulte de 2 ans (F3), un jeune mâle de 18 mois (M2) et une jeune femelle de 7 semaines (F4). La femelle F1 était la mère de M1, M2, F2 et F4. La femelle F2 était la mère de F3; elle donna naissance à un nouveau jeune en juin 1983. Comme le suppose Dittrich (1972), les naissances ont lieu tous les mois de l'année (janvier: 1; février: 1; mars: 1; mai: 1; juin: 1; août: 1; septembre: 2; décembre: 1). Une durée de gestation de 248 jours a été calculée pour la femelle F2, ce qui correspond aux chiffres fournis par Dittrich (223–241 jours). Comme chez *C. zebra* (Schweers 1984), la femelle peut se retrouver en oestrus très peu de temps après avoir mis bas (6 jours chez F2), ce qui correspond vraisemblablement à un oestrus post-partum bien plus précoce que les 4,5 semaines citées par Dittrich.

Les observations ont été conduites en suivant à tour de rôle chaque individu durant une journée complète, exception faite de la longue période de repos de la mi-journée. Durant chaque séjour, chaque animal a été ainsi observé pendant 2 journées espacées l'une de l'autre par 4 jours. Tous les comportements individuels et sociaux ont été décrits, photographiés, comptés et chronométrés.

Résultats

Description des différents comportements

Activité

Dans les conditions de captivité, *C. rufilatus* apparait comme une espèce essentiellement diurne. Lors des visites que nous avons faites au cours de la première moitié de la nuit, tous les animaux étaient inactifs, même par clair de lune; s'ils étaient dérangés par la lumière de la lampe, ils se levaient, mais se recouchaient peu de temps après.

Les maximums d'activité se produisent le matin et en fin d'après-midi, avec une pause plus ou moins absolue en milieu de journée. Chaque animal est généralement actif à 45–70 % de son temps, et il n'apparait pas de différences individuelles notoires, exception faite des jeunes qui sont beaucoup moins actifs que les subadultes ou adultes.

Les repos qui sont pris en cours de journée se passent souvent sous abri, mais ils

peuvent également avoir lieu en plein air et à découvert: milieu de prairie ou pied d'un arbre ou d'un rocher. On compte 5 à 10 places de repos diurne différentes par individu; 1 à 3 d'entre elles sont plus utilisées que d'autres et ce sont alors des places abritées. Les jeunes sont particulièrement fidèles à une place déterminée.

Contrairement à la journée, les places de repos nocturne sont peu nombreuses; ce sont toujours des places abritées et retirées.

Il n'y a aucune place de repos propre à un individu, pas plus qu'il n'existe un quelconque partage du terrain ou une défense d'une zone par un individu quelconque, même lorsqu'il y a un nouveau-né. De jour comme de nuit, le regroupement de 2 ou plusieurs individus dans la même place de repos est donc courante.

Déplacements

L'animal marche la tête et le cou portés à hauteur de garrot; la queue est alors continuellement agitée d'un côté à l'autre. Parfois, il hume en relevant le museau à l'oblique.

L'inquiétude se manifeste par un soufflement qui est répété. L'animal s'arrête, la tête droite, une patte antérieure ou postérieure bloquée en l'air. Une reconnaissance de la source d'inquiétude peut se faire à 10 m de distance, selon un déplacement en demi-cercle, accompagné de soufflements, mais sans tapement du sol. La fuite se fait par une série de bonds allongés, les 2 pattes antérieures puis les 2 postérieures à l'unisson.

C. rufilatus ne possède aucun cérémonial de coucher; à une seule occasion, un individu a brièvement gratté la place. Par contre, tous les individus peuvent gratter le sol de plusieurs coups de leurs pattes antérieures, alternativement ou non, pour chercher à manger. Pour prendre des bourgeons et des feuilles au bout des branches, ils se dressent sur leurs pattes arrières, mais ils ne sont pas capables de maintenir longtemps cette position.

Le jeu est presque exclusivement le propre des jeunes et subadultes. Il est toujours solitaire et principalement à base de course et de saut: l'animal court autour d'un adulte ou d'un obstacle, en effectuant des demi-tours, des sauts sur place ou des bonds allongés.

Miction, défécation, Flehmen

Il n'y a pas d'attitude corporelle notable lors de la défécation où les animaux s'accroupissent très peu, sans avoir ni gratté ni marqué la place, mais souvent après avoir senti le sol. Par contre, pour la miction, la femelle baisse son arrière-train presque jusqu'au sol et le mâle recule fortement les pattes arrières.

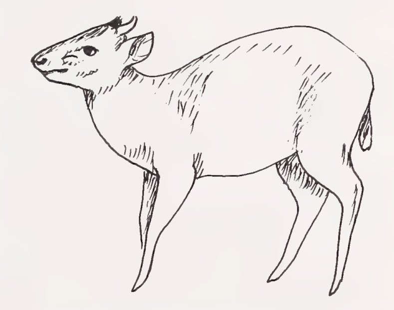


Fig. 1. Flehmen du mâle, la bouche peu entrouverte (dessin d'après photo)

L'urine et les fèces ne sont jamais émis d'une manière dispersée, mais au contraire presque toujours déposés sur certains emplacements situés sur une surface dégagée comme la prairie. Chaque nouvelle émission de fèces se fait donc sur une des zones déjà utilisées à cet effet: 98 % des laissées (342/350) se rencontrent ainsi sur moins de 11 % de la surface de la prairie. Chaque zone représente de 10 à 40 m^2, et comprend de 10 à 70 laissées différentes.

Le Flehmen est uniquement le fait du mâle adulte à l'urine d'une femelle. Au cours de ce comportement, l'attitude corporelle est tout à fait semblable à celle des autres céphalophes: tête droite ou tournée, bouche entrouverte (Fig. 1). Le Flehmen est presque toujours unique et dure peu longtemps: 9,2 secondes $\pm$ 2,0 (N = 16).



Fig. 2. Marquage préorbitaire d'une femelle contre un tronc (dessin d'après photo)

Marquage préorbitaire

Comme tous les Céphalophes, le marquage préorbitaire est un comportement fréquent chez tous les individus qui dispersent ainsi partout où ils passent leurs sécrétions sur tous les supports verticaux, à hauteur de tête. L'individu flaire tout d'abord à petits coups la place à marquer, tête droite, puis il y applique sa zone glandulaire en tenant la tête de côté et il la frotte en ouvrant la bouche et en tirant souvent la langue (Fig. 2). Au lieu de flairer la place, il peut également la lécher ou la gratter avec ses incisives inférieures. Plusieurs marquages peuvent être faits successivement par un même animal à la même place, mais il y a toujours un contrôle du support entre 2 marquages successifs. Les adultes peuvent parfois flairer ou lécher une place sans la marquer, mais ce comportement est plutôt le propre des jeunes qui ne semblent pas marquer avant la 2e année.

81 à 99 % des marquages sont uniques (N = 2887), mais les femelles peuvent répéter leurs marquages plusieurs fois (2 à 6) sur le même site, les mâles le faisant rarement plus de 2 fois. Ces marquages répétés peuvent se faire en utilisant alternativement les 2 côtés de la tête, et à des places différentes. Lorsque 2 individus se trouvent en activité au même endroit, il arrive que le comportement de marquage de l'un incite le 2e à venir marquer aussitôt après sur le même site ou à côté; cela est particulièrement évident lorsque les 2 animaux sont engagés dans un comportement agonistique.

Le marquage préorbitaire a lieu durant toutes les périodes actives de l'individu; il est d'autant plus fréquent que l'animal est excité. On en compte en moyenne de 21 à 60 par heure d'activité, mais les femelles semblent un peu plus actives à ce point de vue que les mâles (respectivement 25 à 60 marquages par h. contre 21 à 34), mais cela peut correspondre dans cet élevage à un niveau de compétition plus grand entre elles qu'entre les mâles. Dans les 2 sexes, la fréquence des marquages croît directement avec l'âge.

Sur ce petit terrain d'environ 0,7 ha, chaque individu utilise de 107 à 175 sites de marquage différents. Là encore, les femelles possèdent plus de sites que les mâles et, chez elles, le nombre varie conformément à l'âge; il en est de même du nombre moyen de marquages sur chaque site: 2,09 à 3,14.

Le degré d'utilisation des différentes portions du terrain pour le marquage préorbitaire est sensiblement le même pour tous les individus: il n'y a pas de zone très marquée par un animal et peu marquée par d'autres. Puisqu'il n'y a pas de partage du terrain entre les divers individus, la grande majorité des sites de marquage sont utilisés en commun. On ne compte que 15 à 30 % des sites qui soient propres à un seul animal et, dans ce cas, leur fréquentation par ce dernier est nettement inférieure à celle des sites communs: 7 à 17 % seulement du total des marquages effectués, soit en moyenne 0,77 à 1,74 par site. Un site utilisé par plusieurs animaux est donc marqué par chaque individu 1,5 à 3,8 fois plus qu'un site propre. Le nombre de marquages par un animal sur un site donné est de même plus élevé lorsque ce site est utilisé par plusieurs individus que s'il n'est fréquenté que par 2 d'entre eux (2 à 3,5 fois plus). La fréquence d'utilisation d'un site de marquage par un individu dépend donc directement de celle des autres animaux.

Globalement, le mâle M1 apparait très stimulé par les sites de marquage des autres animaux: il y marque lui-même 3,1 à 3,8 fois plus que sur ses propres sites; la jeune femelle

F3, par contre, est la moins stimulée par les sites de marquage des autres: elle n'y marque que 1,5 à 1,7 fois plus que sur ses propres sites. Cependant, les sites de F3 sont ceux qui induisent le plus grand nombre de marquages chez les autres animaux, et ceux du mâle M1 le moins; les sites des femelles adultes F1 et F2 sont intermédiaires.

Lorsque 2 individus ont en commun, exclusivement entre eux deux, un certain nombre de sites de marquage, le nombre de ces derniers ainsi que l'intensité des marquages effectués sur chacun d'eux dépendent directement de l'identité des protagonistes. La femelle F1 montre ainsi une forte attirance pour les sites de marquage de la femelle F2; inversement, F2, F3 et M1 montrent tous une préférence pour ceux de F1.

Marquage avec les cornes

Chez *C. rufilatus,* le mâle est le seul sexe à être pourvu de cornes. Cependant, contrairement aux autres espèces de Céphalophes, il marque très rarement avec elles: un seul cas observé sur 128 h d'observation, au cours duquel le mâle avait râclé ses cornes 2 fois de suite contre le bord d'un abri, sans manifester aucun autre comportement annexe, comme un grattage du sol. Il en est probablement de même des femelles, bien que ces dernières puissent frotter parfois leur front et les petits boutons osseux contre différents supports horizontaux ou verticaux, en tournant la tête d'un côté à l'autre; ce comportement n'a été observé que chez la femelle la plus âgée F1 (6 observations), plus rarement chez F2 (2 observations) et jamais chez les autres.

Allogrooming et marquage du partenaire

En dehors des interactions sexuelles ou agonistiques, les contacts corporels entre 2 individus sont de 3 ordres: contrôle olfactif, léchage ou marquage du partenaire.

Deux animaux peuvent se sentir la région nasale, soit que l'un d'eux se soit approché de son partenaire, soit que les deux aient effectué simultanément ce comportement (32 % des 245 contacts observés). Mais le contrôle olfactif du partenaire de loin le plus fréquent se fait dans la région ano-génitale (55 % des contacts), beaucoup plus rarement sur une autre partie du corps comme le garrot, les flancs ou les pattes (13 % des contacts). Les contrôles olfactifs sont toujours brefs; ils sont également peu fréquents, puisqu'ils ne concluent que 20 à 27 % des rapprochements entre individus.

Le léchage est encore plus rare: on en compte en général 2 fois moins que de contrôles olfactifs, en dehors des séquences de poursuite sexuelle ou de comportement maternel. Le léchage du partenaire s'effectue avant tout sur sa région postérieure (zone ano-génitale, queue, croupe: 45 % des observations), antérieure (garrot, face, front ou oreilles: 38 %), mais rarement sur les pattes ou le milieu du corps. Quelques léchages entre femelles font partie du comportement agonistique et mènent directement à la chasse ou à la morsure du partenaire; dans ce cas, ils sont effectués de préférence sur la région postérieure. La totalité des léchages des régions antérieures du partenaire et une partie des autres léchages représentent l'allogrooming. Ce comportement est donc peu fréquent chez cette espèce, puisqu'il n'a été observé qu'à 22 reprises; il est également de courte durée et il n'est jamais réciproque.

Le marquage du partenaire est tout à fait exceptionnel (5 observations) et n'a été observé que chez les femelles. Un individu peut frotter sa glande préorbitaire contre le tarse ou la croupe d'une autre (4 cas); ou bien elle frotte son front contre le corps du mâle (1 cas). Il n'y a donc aucun marquage d'une femelle par le mâle, ni d'un jeune par un adulte. Contrairement à d'autres espèces de Céphalophes, il n'y a jamais de marquage réciproque.

Comportement sexuel

Le mâle adulte pratique un contrôle plus ou moins permanent des différentes femelles en les sentant ou les léchant à la croupe. Il effectue parfois une brève poursuite sexuelle de l'une d'entre elles, même si elle n'est pas réceptive. Il s'approche alors par l'arrière, en attitude étirée, le museau et le cou tenus horizontaux à un niveau plus bas que les épaules, comme le signale Dittrich (1972). Il effectue de nombreux coups de langue à vide (Fig. 3). La femelle fuit en soufflant, la tête basse. Lorsque le mâle parvient à la rejoindre, il tente de la lécher dans la région génitale ou sur les cuisses et il effectue même quelques essais de monte. Ce comportement ne dure généralement guère plus de quelques minutes.

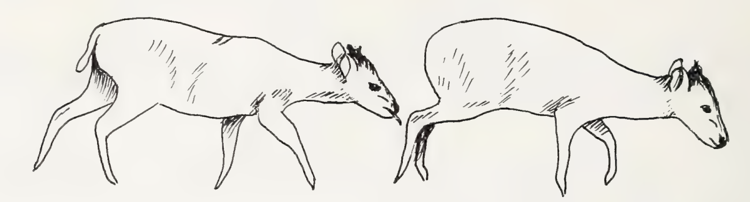


Fig. 3. Poursuite sexuelle. Le mâle effectue un léchage à vide (dessin d'après photo)

Les mêmes éléments fondamentaux de cour se rencontrent lorsque la femelle est proche de l'oestrus, mais ils sont alors beaucoup plus fréquents, les léchages du mâle s'étendant sur toute la région postérieure de la femelle: tarses, zone mammaire. La poursuite est alors soutenue et vive, et se fait parfois à la course. La femelle fuit tête basse en soufflant ou gémissant. Le mâle souffle ou gémit également, la bouche entrouverte; il se lèche souvent la face et les glandes préorbitaires avec de grands coups de langue. La poursuite se fait ainsi en ligne droite ou en arc de cercle, selon des déplacements «en accordéon» du couple, le mâle s'approchant lentement de la femelle en position étirée pour lui lécher l'arrière-train, la femelle fuyant alors vivement. Elle peut durer sans interruption une h ou plus avant qu'intervienne une pause au cours de laquelle le mâle reste fréquemment figé auprès de la femelle, tête et cou horizontaux près de sa vulve, parfois en érection et poussant de petits cris. Après un bref moment d'immobilité, il peut se rapprocher brusquement d'elle en faisant 1 ou 2 petits pas ou piétinements sur place avec ses pattes antérieures. Si la femelle s'est couchée, le mâle reste debout à ses côtés ou se couche lui-même pour peu de temps avant de la faire se lever et repartir. D'autres pauses sont directement provoquées par la miction de la femelle qui induit ainsi régulièrement l'arrêt et le Flehmen du mâle. Si la femelle a réussi à échapper au mâle, ce dernier la retrouve rapidement à la trace.

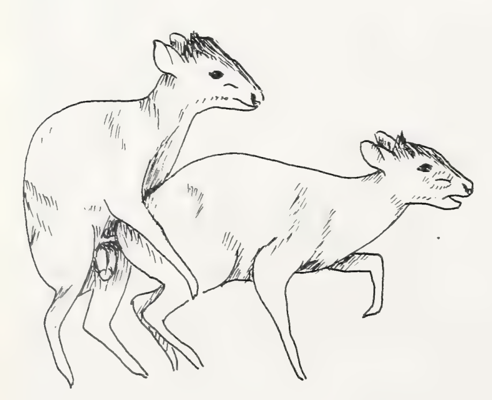


Fig. 4. Monte (dessin d'après photo)

L'intensité du comportement du couple attire fréquemment les autres animaux: jeune venant jouer autour des adultes, femelle adulte venant attaquer celle qui est poursuivie par le mâle ou, au contraire, cette dernière agresse et monte l'arrivante qui peut riposter en tournant sur elle-même et en prenant la position de défense tête basse. Dittrich (1972) note que la femelle en oestrus peut également monter le mâle, de même qu'elle peut le sentir dans la région du pénis ou effectuer quelques mouvements agressifs à son égard (coups de front dans les flancs). Mais, contrairement aux observations de cet auteur de

coups de tête ou de cornes de la part du mâle sur la femelle, nous n'avons jamais observé de gestes agressifs de la part du mâle.

La copulation peut avoir lieu lorsque la femelle ne fuit plus. Avant de monter, le mâle se tiend en érection, la queue écartée en crochet du corps; il lèche le dessus de la croupe et la racine de la queue de la femelle. La monte est brève, tête dressée, museau pointé vers le dos de la femelle. A l'éjaculation, le mâle se redresse plus ou moins à la verticale (Fig. 4); après la démonte, il se lèche le pénis. Plusieurs montes se suivent à bref intervalle, précédées chaque fois par un léchage du dessus de la croupe et de la queue de la femelle.

La réceptivité de la femelle dure 2 jours environ (et non 0,5 à 1 journée, comme le signale Dittrich 1972). Durant toute cette période, la femelle montre un comportement très différent de la normale (Tableau 1). Elle n'est pas plus active que d'habitude, mais elle marque un peu moins et urine, par contre, bien davantage. Elle approche beaucoup moins les autres animaux et est moins souvent approchée par eux (sauf par le mâle). Elle les lèche rarement dans la région antérieure ou moyenne du corps, mais plus souvent au pôle anal; elle n'est plus léchée que par son mâle. Enfin, elle est beaucoup moins agressée par eux et les agresse, par contre, bien plus en donnant beaucoup de coups de tête et en effectuant de nombreuses montes.

Tableau 1. **Fréquence relative des différents comportements d'une femelle avant et pendant sa période de réceptivité au mâle**

(par heure d'activité)

Comportement	non réceptive	début réceptivité	oestrus
% activité	42,5	46,3	53,8
Mictions	0,6	1,1	1,4
Marquages préorbitaires	65,0	46,5	
Approche			
1 femelle	2,7	1,6	0,7
1 mâle	2,4	0	0
Est approchée			
par 1 femelle	3,8	0,8	0,7
par 1 mâle	0,3	très souvent	très souvent
Hume			
1 femelle	1,2	0,3	0
1 mâle	0	0,8	0
Est humée			
par 1 femelle	1,5	0,8	0
par 1 mâle	0	très souvent	très souvent
Est léchée			
par 1 femelle	0,3	0	0
par 1 mâle	0,2	très souvent	très souvent
Agresse			
1 femelle	0,3	0,8	0,5
1 mâle	0	0	0,2
Est agressée			
par 1 femelle	2,1	0,3	0,2

Comportement agonistique

A l'exception des gestes agressifs plus ou moins ritualisés de la femelle en oestrus envers le mâle, les rapports entre individus de sexe différent sont presque toujours pacifiques. Cependant, le mâle adulte peut harceler particulièrement un individu (par exemple la jeune femelle F4, âgée de 10 mois ½), sans que l'on en comprenne les raisons.

Entre femelles, par contre, les explications à tendance agonistique sont habituelles. On peut distinguer par ordre croissant d'agressivité:
– le contrôle et le léchage de la croupe annonçant une morsure ou une chasse.
– la monte.
– le lever: un animal couché est obligé de se lever, pour céder sa place ou fuir, en étant simplement approché par un autre, humé ou touché à la croupe.
– la chasse: un individu poursuit un autre animal au pas ou à la course. Le poursuivi fuit et cherche à se cacher.
– le coup de tête: donné avec le front dans le garrot, le flanc, la croupe ou entre les pattes arrières (Fig. 5). Le mâle peut ainsi frapper de ses cornes.
– la morsure: dans la région anale, sur la croupe, les pattes arrières ou la queue, parfois également sur les oreilles.



Fig. 5. Coup de tête d'une femelle contre l'épaule d'une autre (dessin d'après photo)

Tous ces comportements, exception faite du léchage et des montes agressives absentes chez le mâle, sont présents dans les deux sexes.

Les chasses sont le comportement le plus fréquent (38 à 71 % des interactions agonistiques chez les femelles, 63 % chez le mâle); les coups de tête et morsures viennent ensuite (respectivement 27 et 13 % chez les femelles, 16 % chez le mâle). Le lever hiérarchique est rare (3 à 10 % chez les femelles, 5 % chez le mâle), de même que la monte (3 à 9 % chez les femelles). Ainsi les comportements agonistiques les plus engagés et les plus violents sont généralement les plus fréquents, ce qui est souvent les cas chez les espèces solitaires qui, contrairement aux espèces sociales, ont rarement ritualisé leur comportement agressif.

Chez *C. rufilatus,* il n'y a pas d'attitude démonstrative de menace ou de parade, exception faite de la position défensive décrite plus haut, le front vertical, nez au sol. Un individu est donc directement attaqué par un autre et le seul prémice au comportement agressif de ce dernier est son approche. Si l'individu menacé est supérieur, il ne fuit pas mais menace, tête basse. L'animal dominé cède le terrain, cherche à s'échapper et à se cacher, se couche sur le sol, tête et cou étendus à plat devant lui.

Il n'y a jamais eu de combat proprement dit au sein de cet élevage, mais une explication assez longue entre 2 femelles avait dégénéré en un bref combat frontal, les 2 animaux tournant sur eux-mêmes en cherchant à se frapper sur le corps.

Compte-tenu des comportements agressifs observés, on peut établir l'ordre hiérarchique suivant: mâle M1 > femelle F3 > femelle F1 > femelle F2. La femelle F2 effectue quelques comportements agressifs sur la femelle F1, mais 4 fois moins que l'inverse; la jeune femelle F4 est hors de la hiérarchie femelle et n'est agressée que par le mâle M1.

Vie sociale

Nature et importance des contacts sociaux

En captivité, l'exiguité du terrain contraint les animaux à des contacts auxquels ils échapperaient dans des conditions naturelles. C'est sans doute la raison pour laquelle nous avons observé beaucoup de comportements agressifs, même entre femelles apparentées, ce qui laisse supposer que les femelles filles doivent quitter le domaine ou territoire de leur mère, sans doute au plus tard une fois qu'elles sont devenues adultes. Ceci est encore plus

vrai pour les mâles, puisque les jeunes mâles comme M2 doivent être séparés de leur père. Malgré ces inconvénients, l'observation des animaux libres sur un tel terrain permet de percevoir quelques unes des caractéristiques sociales de l'espèce, principalement en ce qui concerne les possibilités de vie en groupe et le choix des partenaires.

La majorité des contacts sociaux entre individus sont des rapprochements simples, où l'un d'entre eux se dirige vers un autre, passe ou s'arrête auprès de lui (en moyenne 4,1 rapprochements par animal et par heure d'activité). Les contrôles olfactifs sont bien moins fréquents (1,0/animal/heure), suivis par les léchages (0,5/animal/heure) et enfin les comportements agressifs (0,4/animal/heure). Les contacts sociaux sont donc d'autant plus fréquents qu'ils réclament peu d'engagement physique. En prenant en compte toutes les interactions sociales se produisant entre individus, on peut établir une sorte de hiérarchie de l'activité sociale des individus, selon la fréquence des rapports que chacun d'entre eux a avec ses partenaires (par heure d'activité). La femelle la plus âgée, F1, est la plus active (16,2 interactions en moyenne par heure d'activité), et ce niveau d'activité sociale décroit régulièrement avec l'âge chez les femelles: F2 14,3 interactions en moyenne; F3 13,0; F4 2,24. Le mâle adulte M1 se situe à un niveau moyen de 13,7.

Les différentes activités d'un individu donné sont le plus souvent indépendantes de celles des autres. Il est significatif à ce point de vue qu'il n'existe pour ainsi dire pas d'allomimétisme des activités, exception faite lorsque 2 animaux se trouvent directement engagés dans un comportement social précis (agonistique ou sexuel), auquel cas les 2 partenaires effectuent les mêmes comportements à peu près au même moment et au même endroit: marquages, miction, défécation. De même, la rareté des léchages et des marquages d'un autre animal, le caractère le plus souvent unilatéral de ces comportements, la nature essentiellement solitaire des jeux qui ne deviennent jamais contagieux, montrent que chaque individu mène une vie avant tout solitaire, ce qui correspond aux indications que l'on a sur son mode de vie dans la nature. Cependant, plusieurs comportements indiquent l'existence d'une certaine liaison sociale.

Durant la journée, si les individus peuvent prendre des repos isolés en plein air, ils se couchent souvent également dans les abris. Dans ces derniers, ils se reposent en moyenne aussi souvent seuls qu'en compagnie d'un ou plusieurs autres, et la proportion de repos isolés ne varie pas significativement d'un animal à l'autre (40,0 à 66,7 %, N = 287), si ce n'est que les tout jeunes se reposent plus souvent que les adultes dans un gîte particulier. Il n'y a donc ni recherche ni évitement des partenaires pour le repos de jour. Les quelques observations effectuées la nuit par contre, c'est à dire lorsque le niveau général d'activité est réduit ou nul, indiquent que le regroupement des animaux pour le repos est plus fort, puisqu'on rencontre souvent jusque 5 individus couchés dans le même gîte.

Bien qu'ils circulent généralement seuls, les individus sont appelés à se rencontrer fréquemment au cours de leurs activités. Beaucoup de rapprochements sont le fait délibéré d'un animal. En dehors des périodes spéciales comme l'oestrus d'une femelle où la fréquence des rapprochements entre cette femelle et les autres animaux est tout à fait particulière (cf. Tableau 1), les différents individus effectuent globalement le même nombre de rapprochements des autres animaux, exception faite des tout jeunes qui restent le plus souvent couchés à l'écart. Chaque animal est à peu près aussi souvent approché par ses semblables qu'il ne les approche lui-même. La seule différence individuelle se remarque lorsqu'une femelle vient de mettre bas (F1 en septembre, F2 en juin). Dans ce cas, la mère s'approche peu des autres animaux mais elle est, par contre, plus souvent approchée par eux. Le rapport Nombre de rapprochements subis/Nombre de rapprochements initiés passe ainsi de 1,00 à 1,80 chez F1, et de 0,51 à 2,67 chez F2 entre l'époque où la femelle était seule ou gestante et celle où elle possède un jeune. Cela doit correspondre à la tendance naturelle à l'isolement des mères, comme cela existe chez de nombreux ruminants et a été constaté chez *C. monticola* (Dubost 1980).

Il en est à peu près de même pour les contrôles olfactifs d'un autre animal. Mais, si l'on

constate la même inversion du rapport des contrôles olfactifs reçus par rapport à ceux qui sont effectués chez les femelles nouvellement mères comparées aux autres animaux (rapport passant ainsi de 1,16 à 2,46 chez F1, et de 0,51 à 3,49 chez F2), les contrôles olfactifs se distinguent des rapprochements en ce que les mâles effectuent toujours beaucoup plus de contrôles des autres animaux qu'ils en sont l'objet de leur part (4,8 à 5,6 fois plus).

Les contrôles olfactifs sont plus souvent faits par les adultes que par les jeunes, et en particulier par le mâle adulte. Parmi les femelles, le nombre de contrôles effectués croît avec l'âge. Les individues de rang social supérieur contrôlent avant tout leurs partenaires dans la région postérieure du corps (67 % des contacts; N = 164), ce qui correspond peut-être à une persistance des rapports mère-jeune, et ce qui rappelle beaucoup les rapports mâle-femelle; au contraire, 56,1 % des contrôles effectués par des inférieurs sur leurs supérieurs se font dans la région céphalique (N = 82).

Lorsque le contact social est un peu plus engagé comme l'est le léchage d'un partenaire, 3 catégories sociales bien distinctes se dégagent: femelles, jeunes et mâle adulte. Les femelles font beaucoup plus de léchage social que les mâles, et chez elles la fréquence de ce comportement augmente régulièrement avec l'âge, comme pour les contrôles olfactifs. Globalement, chaque femelle effectue autant de léchages des partenaires qu'elle n'est elle-même léchée par eux, mais il faut rappeler que les léchages sociaux ne sont jamais réciproques. Les jeunes animaux lèchent très rarement les adultes, mais ils sont abondamment léchés par eux. Au contraire, le mâle adulte effectue de nombreux léchages des femelles, même en dehors des poursuites sexuelles, mais il n'est jamais léché.

Le léchage d'un jeune par un adulte quelconque se fait presque exclusivement dans la région postérieure (24 observations sur 28). Comme pour les contrôles olfactifs parmi les adultes et subadultes, les animaux supérieurs lèchent surtout l'arrière-train de leurs inférieurs (52,2 % des cas; N = 23), les inférieurs léchant avant tout la partie antérieure du corps de leurs supérieurs (60 %).

Les marquages d'un partenaire au moyen des glandes préorbitaires n'ont été observés qu'entre 2 femelles adultes, la fille F2 ayant marqué sa mère F1 à 3 reprises, cette dernière une seule fois sa fille.

Comme pour le léchage, on reconnait 3 types fondamentaux de rapports sociaux entre les individus, lorsqu'on considère les comportements agonistiques. Les jeunes ne sont pas agressifs et le mâle adulte n'est jamais agressé. La femelle la plus âgée F1 s'est toujours montrée comme la plus agressive, suivie par la jeune femelle F3; par contre, F2 était de loin la plus agressée. Globalement, les 2 femelles les plus âgées (F1 et F2), c'est à dire les 2 femelles ayant des jeunes, sont les individus les plus souvent impliqués dans des explications agonistiques avec un autre animal, mais surtout entre elles-mêmes. Il n'apparait pas, cependant, qu'une femelle nouvellement mère connaisse un surcroît d'agressivité à l'égard de ses semblables, puisque le comportement de ces 2 femelles n'a jamais varié en conséquence.

Préférences sociales

L'observation du comportement des différents individus de cet élevage, qui se trouvaient étre tous directement apparentés les uns aux autres comme le sont sans doute la plupart des unités sociales dans la nature, nous permet de mettre en évidence certaines préférences (Tableau 2).

La femelle F1, la femelle la plus âgée et, directement ou indirectement, la fondatrice de ce groupe d'animaux, effectue une grande partie de ses léchages sur sa fille F4 encore immature. Elle semble cependant marquer une nette préférence sociale pour sa fille adulte F2, auprès de laquelle elle se repose souvent (comme d'ailleurs auprès du mâle adulte M1); elle la recherche, la contrôle et la lèche plus souvent que les autres. Cependant, les rapports qu'elle entretient avec elle sont surtout de nature agressive.

La femelle adulte F2 lèche beaucoup sa jeune «soeur» F4. Elle se repose souvent en compagnie de sa fille subadulte F3 qu'elle recherche et lèche plus fréquemment que les

Tableau 2. **Préférences sociales: % de comportements adressés par un animal à un autre**

Receveur	Comportement	Initiateur				
		Femelle F1	Femelle F2	Femelle F3	Femelle F4	Mâle M1
F1	Repos		24,4	16,0	20,0	31,4
	Rapprochement		28,1	43,1	?	41,4
	Flairer		43,6	32,4	31,3	31,9
	Lécher		6,3	40,0	0	81,3
	Agresser		100,0?	55,6	0	5,0
F2	Repos	30,6		34,0	23,3	28,6
	Rapprochement	36,2		22,5	?	21,1
	Flairer	50,8		41,2	31,3	36,2
	Lécher	18,2		40,0	?	12,5
	Agresser	98,6		44,4	0	5,0
F3	Repos	22,2	37,8		46,7	31,4
	Rapprochement	24,6	33,3		?	27,3
	Flairer	16,4	25,6		6,3	21,3
	Lécher	4,5	18,8		0	6,3
	Agresser	1,4	0		0	5,0
F4	Repos	16,7	15,6	28,0		8,6
	Rapprochement	13,0	2,1	2,0		10,2
	Flairer	18,0	10,3	2,9		10,6
	Lécher	77,3	75,0	20,0		0
	Agresser	0	0	0		85,0
M1	Repos	30,6	22,2	22,0	10,0	
	Rapprochement	26,1	36,5	32,4	?	
	Flairer	14,8	20,5	23,5	31,3	
	Lécher	0	0	0	0	
	Agresser	0	0	0	0	

autres animaux. Ses rapports envers sa mère F1 sont pacifiques (contrôles olfactifs) ou agressifs.

La femelle subadulte F3 se montre plus attirée par les 2 femelles adultes précédentes que par le mâle adulte ou la jeune femelle F4. Elle se repose fréquemment auprès de sa mère F2, mais recherche beaucoup sa grand-mère F1 lors des activités. Avec ces 2 femelles adultes, ses rapports sont à la fois pacifiques (contrôles olfactifs, léchages) et agressifs.

La jeune femelle F4 se repose surtout en compagnie de F3, c'est à dire l'autre jeune femelle non suitée, mais elle contrôle fréquemment tous les adultes.

Quant au mâle adulte, il ne montre pas de préférence nette pour un animal donné ni pour ses repos, ni pour ses contrôles olfactifs, ni pour ses contacts pacifiques ou agonistiques. Cela laisse présager que cette espèce ne vit pas en couple et que, dans la nature, un mâle aurait un domaine recouvrant ceux de plusieurs femelles. Cependant, à l'égal d'autres espèces solitaires comme *Muntiacus muntjak* et *M. reevesi* (Dubost 1970, 1971) et peut-être *Hydropotes inermis* (Feer 1982), on remarque chez lui, au niveau des rapprochements et des léchages, une certaine préférence pour la femelle F1, c'est à dire la plus âgée et celle qui a la plus forte descendance. Faute d'observations effectuées en liberté, nous ne savons pas si cette même préférence existe dans des conditions de vie naturelle et si elle représente un rudiment de vie de couple. Cependant, la femelle *C. rufilatus* est capable de connaitre un nouvel oestrus après la mise-bas (4,5 semaines selon Dittrich 1972; mais 6 jours seulement selon nos propres observations). Cela explique peut-être pourquoi le mâle M1 a montré une forte préférence pour la femelle F1 en septembre 1982, 7 semaines après que cette femelle ait mis bas son jeune F4, alors qu'en juin 1983, la femelle F2, qui avait mis bas 8 jours auparavant, se trouvait à son tour la principale cible des rapprochements de la part du mâle.

Les rapports existant entre les 3 femelles F1, F2 et F3 dénotent à la fois une recherche pacifique du partenaire et un comportement agressif d'éloignement. Les 2 mères F1 et F2 ont des rapports plus souvent agressifs que pacifiques: en moyenne, 74,7 % des comportements agressifs ou menant à une agression effectués par la femelle F1 envers les autres animaux ont été dirigés sur la femelle F2 contre 28,3 % seulement de ses comportements pacifiques, et 71,8 % des comportements agressifs de F2 ont été adressés à F1 contre 19,6 % des comportements pacifiques. Vis à vis de la femelle subadulte F3, les rapports des 2 femelles adultes F1 et F2 sont, au contraire, plus pacifiques qu'agressifs: 17,1 % des comportements pacifiques contre 8,9 % des comportements agressifs de F1 se sont portés sur F3; 30 % des comportements pacifiques contre 12,8 % des comportements agressifs de F2 ont été adressés à F3. Le même phénomène, encore plus accusé, est valable pour les rapports de F1 ou F2 avec la jeune femelle F4: 35,7 % contre 9 % pour F1 vis à vis de F4, et 30,9 % contre 5,2 % pour F2 vis à vis de F4.

Par contre, la femelle subadulte F3 entretient avec les femelles adultes F1 ou F2 des rapports déjà plus agressifs que pacifiques: 44 % contre 33 % vis à vis de F1, et 43 % contre 32 % vis à vis de F2. Il apparait donc que l'importance des rapports agressifs entre femelles croît avec l'âge de la fille et est surtout le propre de cette dernière, puisque les adultes se montrent toujours beaucoup plus pacifiques envers elle. Il se pourrait donc que, dans la nature, ce comportement engendre l'isolement spatial des mères et filles, une fois ces dernières devenues adultes.

Discussion

Il est couramment admis que les Céphalophes et Néotraginés africains représentent les équivalents des Cervidés forestiers d'Asie ou d'Amérique du sud. En fait, cette ressemblance est, le plus souvent, beaucoup plus apparente que réelle et ne semble être que le résultat des fortes contraintes physiques du milieu qui modèlent obligatoirement les organismes. En pratique, le groupe des Céphalophes africains est bien plus riche que les autres groupes équivalents des autres continents, puisqu'il comprend souvent 4–6 espèces sympatriques bien séparées écologiquement les unes des autres, 1 ou 2 d'entre elles étant même plus ou moins spécialisée à un biotope particulier, alors que les Cervidés de même poids n'ont qu'1 ou 2 formes à écologie assez générale. Les connaissances des Cervidés sud-américains ne sont pas suffisantes pour que l'on puisse établir une comparaison entre eux et les Céphalophes, et il en est de même de la plupart des espèces asiatiques. Mais, si l'on considère le genre *Muntiacus,* et principalement *M. muntjak* qui peuple les forêts indomalaises (Barrette 1977; van Bemmel 1952; Blanford 1888–91; Dubost 1971; Lydekker 1924; Prater 1965), on constate que *C. rufilatus* est le Céphalophe qui se rapproche le plus de cette espèce par:

- sa taille: 10–14 kg contre 15–35 kg
- sa coloration: corps rougeâtre, front et pattes gris-noirâtres chez les 2 espèces
- ses appendices frontaux: présents seulement chez les mâles, réduits à de petits boutons osseux chez les femelles
- son rythme d'activité: à prédominance diurne, mais également actif de nuit
- ses biotopes: de la grande forêt à la forêt claire, avec une utilisation fréquente des zones découvertes
- son régime alimentaire mixte: fruits, feuilles, parfois herbe
- son comportement agonistique: coups de tête et morsure chez les mâles comme chez les femelles
- son mode de vie sociale: surtout solitaire, mais regroupement possible de plusieurs individus. En captivité, forte intolérance des mâles, cohabitation des femelles avec agression caractérisée entre certaines.

L'équivalence physique et écoéthologique entre ces 2 espèces semble donc assez grande,

bien qu'il persiste certaines divergences, surtout en ce qui concerne le comportement social: mode de marquage du domaine, importance de l'allogrooming réciproque et du marquage des partenaires, *M. muntjak* se montrant nettement plus riche dans ses relations interindividuelles.

Cependant, dans bien des comportements, *C. rufilatus* est tout à fait semblable aux autres Céphalopes déjà étudiés comme *C. monticola* et *C. dorsalis* (Dubost 1983), et cela atteste de la grande homogénéité du genre *Cephalophus,* au moins en ce qui concerne les comportements de base (attitudes corporelles). Chez ces 3 espèces de Céphalophes, comme chez toutes celles observées, on retrouve, en effet, le même schéma fondamental lors du coucher: simple, sans cérémonial annexe (également chez *C. callipygus* et *nigrifrons,* obs. pers.); – lors de la recherche de la nourriture: parfois avec grattage du sol ou lever sur les pattes arrières (également chez *C. maxwelli,* Hopkins 1966; *C. callipygus* et *nigrifrons,* obs. pers., Kingdon 1982); – lors de l'alarme: corps bloqué à l'arrêt, une patte antérieure levée (Walther 1979; également chez *C. callipygus* et *nigrifrons,* obs. pers.); – lors de la miction et de la défécation: attitudes engagées pour la miction mâle ou femelle, mais non pour la défécation, sans comportement annexe et sans dissémination des laissées (également chez *C. callipygus* et *nigrifrons,* obs. pers.; *maxwelli,* Aeschlimann 1963; *harveyi,* Kingdon 1982); – lors du Flehmen: bref, bouche peu entrouverte, présent seulement chez le mâle, le plus souvent unique (également chez *C. maxwelli,* obs. pers., Aeschlimann 1963); – lors du marquage préorbitaire: frottement contre un support vertical, dispersé partout, présent dans les 2 sexes, le plus souvent unique (également chez *C. callipygus* et *nigrifrons,* obs. pers.; *maxwelli,* Aeschlimann 1963; Ralls 1974); – lors de la poursuite sexuelle: en ligne ou en cercle, léchage abondant de la région postérieure de la femelle, position étirée du mâle en Überstrecken, soufflements des 2 partenaires, comportement agressif plus ou moins ritualisé de la femelle sur le mâle (également chez *C. zebra,* Schweers 1984), copulation brève avec la tête dressée (également chez *C. maxwelli,* obs. pers.; *nigrifrons,* Walther 1979); – lors des rapports agonistiques: absence d'attitudes de menace ou de parade (également chez *C. maxwelli,* Ralls 1975), posture défensive nez au sol, front vertical (également chez *C. nigrifrons,* Walther 1979), soumission tête et corps aplatis sur le sol.

Cependant, entre ces 3 espèces comme entre d'autres, apparaissent certaines différences qui sont le reflet des divergences dans les modes de vie (biotopes, rythmes d'activité), et qui s'inscrivent en majorité dans le comportement social (Tableau 3). Dans la plupart des cas, *C. rufilatus* est placé à mi-chemin entre l'espèce diurne *C. monticola* et l'espèce nocturne *C. dorsalis:* sur 36 caractères analysés, 16 sont directement intermédiaires entre ceux de ces 2 espèces, 6 correspondent davantage à ceux de la forme diurne et 8 à ceux de la forme nocturne. Il apparait ainsi que ces modifications comportementales semblent la conséquence directe du changement de rythme d'activité (Dubost 1983). Sur 6 caractères seulement, *C. rufilatus* se distingue nettement de *C. monticola* et *dorsalis:* absence de jeux sociaux, absence d'allogrooming réciproque, nombreux comportements agonistiques entre animaux apparentés, présence de morsure, monte des autres animaux par une femelle en oestrus, défécation localisée. Exception faite de la morsure qui existe aussi chez *C. zebra* et *nigrifrons* (Walther 1979; Schweers 1984), tous ces comportements apparaissent pour l'instant comme caractéristiques de l'espèce *rufilatus.* Deux d'entre eux doivent être particulièrement notés.

La relative bonne entente des femelles en captivité joint au fait que, contrairement à toutes les autres espèces congénériques, les femelles sont totalement inermes, peut nous faire supposer que l'espèce pourrait ne pas montrer de territoire femelle, contrairement à ce qui est connu chez *C. monticola* et ce qui est peut-être le cas de *C. maxwelli* (Aeschlimann 1963), *callipygus* et *dorsalis* (obs. pers.).

C. rufilatus utilise volontiers en captivité, comme dans la nature selon les quelques observations disponibles, les surfaces plus ou moins découvertes; il mange de l'herbe et est

Tableau 3. **Variabilité comportementale entre différentes espèces de *Cephalophus***

	C. monticola	*C. rufilatus*	*C. dorsalis*	autres espèces
Milieux	forêt ombrophile	forêt claire, galerie forestière, bordure de forêt	forêt ombrophile	
Caractéristiques physiques				
Poids corporel	4–6 kg	10–14 kg	19–25 kg	
Présence de cornes	♂–♀	♂	♂–♀	♂–♀
Activité				
Rythme	diurne	diurne-nocturne?	nocturne	diurnes: *callipygus, leucogaster, nigrifrons* (3); *adersi, natalensis* (5) diurne-nocturnes: *maxwelli* (1), *sylvicultor* (3), *harveyi* (5) nocturnes: *niger* (2), *spadix* (5)
% de temps actif	67–76 %	45–70 %	33–54 %	
lieu de repos	à découvert	à découvert ou caché	le plus souvent caché	
Attitudes				
attitudes corporelles	accusées	simples	simples	
repos sur les carpes	–	–	+	–: *callipygus,* +: *nigrifrons* (3)
déplacements	tête horizontale	tête horizontale	tête horizontale ou basse	tête horizontale: *callipygus, maxwelli, nigrifrons* (3) tête horizontale ou basse: *sylvicultor* (3)
Informations visuelles				
Reconnaissance à distance	bonne	moyenne	mauvaise	bonne: *callipygus, nigrifrons* (3) mauvaise: *sylvicultor* (3)
Signal corporel optique	+	–	–	– chez les autres espèces, sauf *maxwelli* (1)
Marquage avec les cornes	♂–♀	♂–♀? (rare)	–	♂ *maxwelli,* ♂–♀ *callipygus,* ♀ *nigrifrons* (3)
Informations olfactives				
Hume l'air	–	rare	+	+: *nigrifrons* (3)
Défécation en tas	–	+	–	–: *callipygus, nigrifrons* (3)
Marquage préorbitaire	♂–♀–j	♂–♀	♂	♂–♀ *maxwelli* (1,7); ♂–♀ *callipygus,* ♀ *nigrifrons* (3)
Informations acoustiques				
Cri de contact	plus ou moins permanent	répété lors des rapprochements	unique lors des rapprochements	
Soufflement d'inquiétude	+	+	–	+: *callipygus* (3)
Sifflement d'alarme	+	–	Rare	+: *maxwelli* (1); *callipygus* (3); *nigrifrons, sylvicultor* (5)
Tapement du sol avec les pattes	+	–	Rare	+: *callipygus* (3)
Jeux				
Eléments	Course, saut, ruade, marquage, monte, combat	Course, saut, marquage, combat	Course, saut, combat	

Tableau 3 (countinued)

	C. monticola	*C. rufilatus*	*C. dorsalis*	autres espèces
Fréquence	+	–	–	
Participants	Jeunes et adultes	Jeunes	Jeunes	
Jeux sociaux	+	–	Rares	+: *maxwelli* (1); *callipygus, nigrifrons* (3)
Contacts avec 1 partenaire				
Allogrooming réciproque	+	–	Rare	+: *maxwelli* (1,7); *callipygus, nigrifrons* (3)
Marquage du partenaire	+	Rare	–	+: *callipygus* (3); *zebra* (9)
Marquage du jeune	–	–	–	+: *maxwelli* (1); +/–: *zebra* (4,9)
Marquage réciproque	+	–	–	+: *maxwelli* (1,7), *zebra* (9)
Poursuite sexuelle				
Laufschlag	+	Ebauché	–	+: *zebra* (9); *nigrifrons* (10, 11)
Pose menton/croupe	–	–	+	+: *sylvicultor, zebra* (9)
Remontée latérale du mâle	–	–	–	+: *zebra* (97
Comportement agressif du mâle sur femelle	+	–	–	+: *rufilatus* (2), *dorsalis* (4), *maxwelli* (6), *zebra* (9)
Monte des autres animaux par la femelle	–	+	–	
Arrêt de la femelle pour la copulation	–	–	+	
Comportement agonistique				
Marquage mutuel	–	–	?	+: *maxwelli* (9)
Morsure	–	♂–♀	♀? (ritualisé)	+: ♂ *zebra* (9); ♀ *nigrifrons* (11)
Coups de front ou cornes	♂–♀	♂–♀	+?	+: ♂–♀ *maxwelli* (8); ♂ *zebra* (9)
Vie sociale				
Goupement en nature	1–4	1 (2–3?)	1	1–4: *maxwelli* (1); *natalensis, sylvicultor* (5)
Groupement en captivité	+	+/–	–	
Allomimétisme	+	Rare	–	
% de repos du mâle avec les femelles	75 %	42 %	≏0 %	

(1): Aeschlimann 1963; (2): Dittrich 1972; (3): obs. pers.; (4): Frädrich 1964; (5): Kingdon 1982; (6): Ralls 1970; (7): Ralls 1974; (8): Ralls 1975; (9): Schweers 1984; (10): Walther 1968; (11): Walther 1979

attiré par les pierres à sel. Ceci le différencie beaucoup des espèces forestières proprement dites que nous avons observées (*C. monticola, nigrifrons, dorsalis* et *callipygus*). C'est donc une espèce beaucoup plus savanicole que les autres; et il est à prévoir que son comportement consistant à concentrer fortement ses laissées sur de petits emplacements, comme il apparait en captivité, doit également se rencontrer dans la nature, puisqu'un tel mode de dépôt des fèces est presque toujours la caractéristique d'animaux de régions ouvertes.

Globalement, le genre *Cephalophus* se montre donc à la fois très homogène dans ses comportements fondamentaux plus ou moins fixes comme les modes de locomotion, d'excrétion, de marquage, de reproduction, etc., et très variable dans les comportements qui subissent une certaine variation selon les conditions de vie. Cela corrobore précisément les résultats obtenus à partir des caractéristiques physiques, puisqu'on rencontre toujours chez eux, à côté du même schéma de base, de nombreuses modifications selon les préférences écologiques ou le rythme d'activité. Ainsi peuvent coexister des caractères que l'on peut interpréter comme «archaiques» ou, au contraire, «évolués» (Dubost 1983). Mais

cette variabilité au sein du même genre nous oblige à reconsidérer la valeur phylogénétique et évolutive de certains comportements, puisque nous n'avons aucun argument pour décider si, à l'intérieur de ce genre, une ou plusieurs espèces sont plus avancées que d'autres. Au vu de la dualité d'expression qui peut se manifester lors du comportement sexuel (présence ou non de Laufschlag ou de pose du menton sur la croupe), du comportement agonistique (coups de front seuls ou présence simultanée de coups de front et de morsures), ou du comportement social (vie solitaire ou vie plus ou moins permanente avec 1 ou plusieurs partenaires, léchages et marquages mutuels absents ou fréquents, allomimétisme ou non dans les activités, etc. . . .), il semble bien que le genre *Cephalophus* se trouve placé à un carrefour évolutif. Chez lui, des comportements très «avancés» peuvent ainsi apparaitre selon les espèces et leurs conditions de vie, et il ne semble plus possible de considérer les Céphalophes comme les Bovidés les plus primitifs.

Remerciements

Nous remercions vivement Mr et Mme Saint-Pie pour leur accueil et les facilités qu'ils nous ont offertes lors de nos séjours au Zoo de Piétat.

Zusammenfassung

Verhaltensunterschiede innerhalb der Gattung Cephalophus (Ruminantia, Bovidae) am Beispiel von C. rufilatus Gray, 1846

Im Zoo von Pietat konnte eine auf einem 0,7 ha großen Gelände freilebende Gruppe von 7 *Cephalophus rufilatus* ethologisch untersucht werden. In den meisten seiner Verhaltensweisen unterscheidet sich diese Art nicht von den anderen bereits untersuchten Duckern. Jedoch zum Unterschied von eben diesen Arten zeigt *rufilatus* ein fast völliges Fehlen sozialen Spieles und des sich gegenseitigen Putzens. Vorhanden sind dagegen Beißen und Kopfstöße im Verlauf agonistischer Auseinandersetzungen. Der Laufschlag ist nur rudimentär vorhanden. Das in Brunft befindliche Weibchen besteigt häufig die Gruppenmitglieder. Die Defäkation erfolgt stark lokalisiert in Häufchen. Global betrachtet ist *rufilatus* eine Art mit Tag-Nacht-Rhythmus und zeigt dementsprechend auch ein intermediäres Verhalten. Dies zeigt sich besonders im Sozialverhalten, denn die einzelnen Individuen vertragen sich relativ gut, wenngleich auch jedes Tier seine eigene von den anderen unabhängige Aktivität hat und mit diesen nur ein Minimum inter-individuelle Kontakte hat. Es scheint keine bestimmte Wahl des Partners zu bestehen.

Im großen und ganzen erscheint die Gattung *Cephalophus* relativ homogen in bezug auf fundamentale Verhaltensweisen wie Fortbewegung, Sekretausscheidung, Markierung, Fortpflanzung, usw. Unterschiede dagegen findet man bei allen den Lebensstil betreffenden Verhaltensweisen im Biotop und bei den Aktivitätsrhythmen. Dies alles entspricht recht gut der morphologischen und ökologischen Variabilität dieser Gruppe. Neben Merkmalen, die man als «ursprünglich» bezeichnen kann, findet man auch gewisse höher entwickelte Verhaltensweisen. In diesem Kontext erscheinen die Cephalophinae innerhalb der Bovidae keineswegs als eine der primitivsten Gruppen.

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Z. Säugetierkunde 53 (1988) 48–54

ISSN 0044-3468

Systematics and chromosomes of the Indian gazelle, *Gazella bennetti* (Sykes, 1831)

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Receipt of Ms. 15. 1. 1987

Abstract

In 3 individuals of *Gazella bennetti* chromosome numbers of 2n = 50 (♀) and 51 (♂) were found. The structures of the X and Y1 chromosomes differ from other gazelle species. The Indian gazelle must not be classified as a subspecies of *G. gazella* or *G. dorcas.*

Introduction

The genus *Gazella* de Blainville, 1816, has always been a major challenge to the mammalian taxonomist. There is still room for subjectivity in the classification of some members of this group, not only at the subspecies but even at the species level. No common agreement has yet been reached on the number of genuine species within this genus, especially with regard to the "smaller gazelles" (which exclude the subgenus *Nanger*). For example, no final answer can be given to the question whether *Gazella leptoceros* should be regarded as a species of its own or whether it should be incorporated into *Gazella subgutturosa* (as proposed by Lange [1972]). Another gazelle with an uncertain taxonomic position is the Chinkara or Indian gazelle, *Gazella bennetti* (Sykes, 1831), which was included into *Gazella gazella* by some authors, whereas others considered it as belonging to *Gazella dorcas* (see below for further discussion). As will be shown in this article, neither of these views is correct.

Some of the uncertainties about the classification of smaller gazelles are due to the fact that variation within the units commonly regarded as species, is almost as big as the total range of variation within the remarkably uniform subgenus *Gazella.* There is such an overlap between intra- and interspecific variation both in coloration and cranial morphology that geographical provenience of an individual specimen is often the most important character for its classification – which is certainly not the correct procedure for taxonomic identification. This is particularly true due to human interference with the distribution of gazelles in recent years. Gazelles are favorite pets all over the Middle East and North Africa and there is a flourishing, yet completely uncontrolled trade of live animals over long distances. Thus, the locality where a specimen was obtained by a zoological collector may be far away from the place of origin of the animal. In addition, the trade and keeping of gazelles in one's backyard has an immanent danger of hybridization, which adds to the difficulties of classification.

One possibility to decrease the difficulties of gazelle systematics is to establish the exact geographical ranges of defineable forms prior to the distortions caused by human interference. Bone remains of gazelles are common finds at most archaeological sites in the Middle East and North Africa. Once they can be identified beyond the genus level, these finds have a potential to determine the original range of the respective species. However, except for complete skulls or well preserved fragments thereof, specific identification of isolated gazelle bones is still impossible. To establish criteria for the identification of postcranial bones (apart from the evaluation of differences in absolute size which may have shifted during the recent geological past), it is necessary to increase the number of well identified

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reference skeletons. Obviously, this necessity, namely correct taxonomic identification of the reference specimen, brings us back to the difficulties described above.

This article is a first result of some work based on the attempt of one of us (H.P.U.) to build up a comparative collection of gazelle skeletons for palaeo-zoological research. Fairly large breeding groups of different gazelle species kept under the medical care of another of us (C.W.F.) at the zoo of Al-Ain (Abu Dhabi, U.A.E.) were a source not only of skeletal material, they also provided the living tissues to try a 'biological' determination of the taxonomic affinities of the respective populations. As a basic approach, some karyological research was started by the third member of our group (H.T.). It is mainly due to this last part of our work that some contributions to the systematics of gazelles have resulted from this effort. Some gazelles brought from Pakistan to the zoo of Al Ain gave surprising results when tested for their chromosome numbers. Some conclusions on the systematic position of these gazelles will be based on a description of the animals themselves and on the evaluation of their karyotypes.

Material and methods

A group of gazelles captured during a hunting expedition in Pakistan was brought to the zoo of Al-Ain in Abu Dhabi (United Arab Emirates) in 1984. Unfortunately, the exact geographical origin of the animals could not be investigated. It was obvious, however, that they were "chinkaras", which is the local name for the Indian gazelle, *Gazella bennetti.*

The general colour of the animals is a light fawn, almost isabelline. The stripe along the flank is brown, narrow at its origin on the shoulder but increasing in width as it extends along the lower part of the rump. The upper rim of this stripe is not well defined nor is there a well marked zone of lighter coloration above the flank stripe. The lower border of the flank stripe is well marked against the yellowish colour of the ventrum which also extends along the inner thighs of the legs. Like the flank stripe, the pygal stripe is brown, fading into the fawn colour of the back, but contrasting well with the whitish patch on the inside of the thighs. The pygal stripe extends down the sides of the tail, ending in the black of the distal portion of the tail. Other spots of dark coloration are just above the hoofs, particularly between the two digits, and the carpal brushes. The facial stripes are also dark brown in colour, extending from the anterior corner of the eyes finishing just distal to the upper lips. Above and below these stripes, as well as around the eyes and the mouth, the colour is very light. The nasal area between the facial stripes is fawn with a typical dark nose blotch of varying extent. In some animals it is an ill defined brown spot only. Usually it is almost black in the middle with shades of brown towards the edges. Between the eyes, the colour is reddish-fawn. Darker eyebrow stripes reach from the eyebrows to the lateral edges of the horns, fading toward the base of the large ears. The frontal region is lighter again, though not much different from the general colour of the animal.

Compared to most other gazelle species, the markings of our animals are fairly unconspicuous. This is a known feature of *Gazella bennetti.* In comparison to typical Indian animals of this species, our animals are less reddish, more greyish in total appearance. Specimens from Baluchistan, originally considered to be a separate species (*Gazella fuscifrons,* Blanford, 1873), have a dark coloration of the forehead, not present in our animals. The description available for *Gazella bennetti christyi* Blyth, 1841, which is the subspecies inhabiting the intermediate zone between the two extremes, is too vague to be applied. The "silvery drab-brown" (Groves 1985) of this subspecies might in fact apply to our animals. However, they could also be called "rich tobacco-brown" which – according to Groves (1985) – is the coloration of the unnamed subspecies inhabiting the Salt Range and Punjab areas of northeastern Pakistan and northern India. Thus, the better known subspecies *bennetti* and *fuscifrons* can both be excluded, whereas the two less well known races of Pakistan are both possible identifications for the animals used here.

For karyotyping, the blood of three animals was tested: An adult female and its male calf, and an unrelated adult male. Blood samples of 3–5 ml were sent in a heparinized form from Al Ain to Tübingen by air courier. The time span between taking the blood samples and the beginning of cell cultivation was 48 to 60 hours. Cell culture was carried out by isolating lymphocytes over a ficoll paque gradient, and stimulation of mitoses with phytohemagglutinine in RMPI 1640 medium with 15 % fetal calf serum. After 72 hours of culture at 37 °C, 5 % CO_2, mitoses were arrested with colchicine. Metaphase chromosome spreads were prepared after hypotonic treatment and fixation in methanol/acetic acid (3:1) by routine air dry techniques. For identification, the metaphases were stained with orcein, and for the characterisation of constitutive heterochromatine, the C-banding technique was used (Sumner 1972).



Fig. 1. Young male of *Gazella bennetti* from Pakistan in the quarantine station of Al Ain Zoo

Results

For the three animals under consideration we found a diploid chromosome number of 2n = 50 (♀) and 2n = 51 (♂). The autosomes are formed by 4 pairs of individually distinguishable metacentric and 20 pairs of telo- to acrocentric chromosomes. The last ones have very minute p-arms, and only in metaphases with long, slightly condensed chromosomes could the p-arms be identified. Satellites were sometimes visible in these metaphases at the end of the q-arms of some of the largest acrocentric chromosomes. No further grouping of the autosomes was possible after orcein staining (fig. 2).

The heterosomes are 2 submetacentric X-chromosomes in the female, and one X, a submetacentric Y1 and an acrocentric Y2 chromosome in the male. The X is the largest of all chromosomes, containing about 14 % of the total chromosome length. Its p:q ratio is just 1:2. The Y1, also with a p:q ratio of 1:2, was individually identifiable even after orcein staining alone. Y2 could not be distinguished from other acrocentrics of similar length after orcein staining.

C-banding reveals constitutive heterochromatine at the kinetochore regions of all the autosomes. Two pairs of telocentric chromosomes exhibited heterochromatine at their telomeres. Most striking was the observation of constitutive heterochromatine accumulated along the total length of the p-arms of the X and Y1 chromosome (fig. 3).



Fig. 2. Karyotype of *Gazella bennetti*, orcein stained

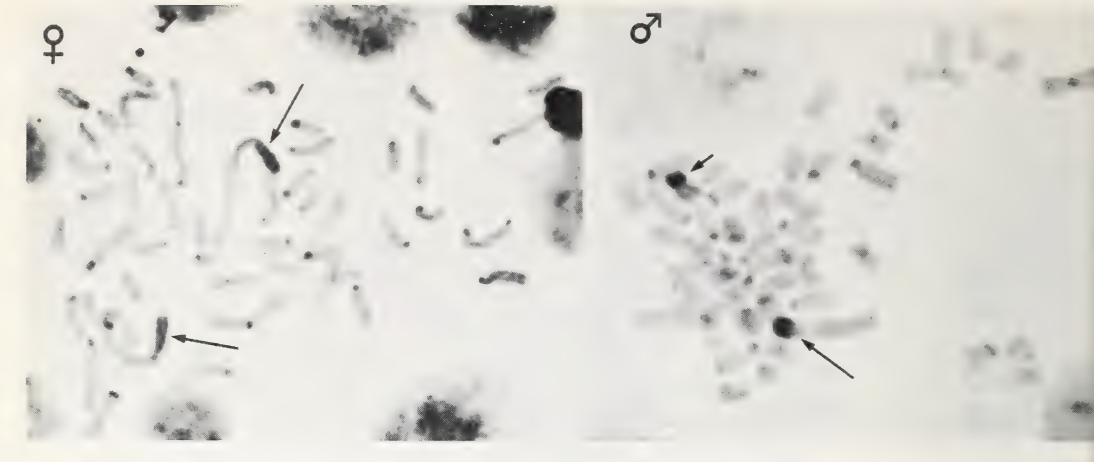


Fig. 3. C-banded chromosomes of a female and a male individual of *Gazella bennetti.* The arrows point to the heterochromatic arms of the X chromosomes and to the Y1 chromosome (short arrow)

Discussion

There are three points of interest in comparing the karyotype of *Gazella bennetti* with published karyotypes of other members of the genus *Gazella* (Hsu and Benirschke 1967/77; Wurster 1972; Effron et al. 1975; Benirschke et al. 1984): 1. the chromosome number, 2. the shape of the X and Y1 chromosomes with a p:q ratio of 1:2, and 3. the amount of constitutive heterochromatine in the p-arms of X and Y1 which all differ greatly from those previously described.

The high chromosome number of 2n = 50 ♀/51 ♂ of *Gazella bennetti* is only outdone by 2n = 58 in both sexes of *Gazella thomsoni* (Hsu and Benirschke 1968). The autosomes of this species are all telo- to acrocentric. Of the other gazelles. *Gazella dama* with 38–40 chromosomes in the female and 39–40 in the male (Benirschke et al. 1984) is nearest to *Gazella bennetti.*

Varying chromosome numbers due to Robertsonian fusions/fissions in a zoo population of *Gazella soemmeringi* were published by Benirschke et al. (1984). In the case of *Gazella bennetti,* multiple fissions of different metacentrics may have lead to the numbers found in our investigations. Such a process could even have started from a chromosome number as low as the ones found in *Gazella granti* or *Gazella subgutturosa.* The 14 pairs of metacentrics of the latter species could be translated – by 10 fissions – into 4 remaining metacentrics and 20 acro- to telocentric pairs as observed in the investigated animals. A detailed analysis of the chromosomes by other banding techniques, which gives further evidence for this hypothesis, will be published separately. Because of the small number of individuals available, no comment is possible on the natural variation in chromosome numbers in *Gazella bennetti.*

The two other points of interest characterising the karyotypes of the investigated animals are of importance in considerations on the systematic position of *Gazella bennetti.* An X chromosome of comparable length with a similar p:q ratio is present in *Gazella subgutturosa, Gazella leptoceros, Gazella gazella, Gazella granti,* and *Gazella dama.* Only for the first three species have there been reports that the Xp behave heterochromatic. A

meta-submetacentric Y chromosome is found in *Gazella soemmeringi* (Benirschke et al. 1984), but nothing was published on its content of heterochromatin. Constitutive heterochromatine in a Y chromosome (either Y1 or Y2) has only been demonstrated for the acrocentric Y1 of *Gazella subgutturosa* (Hsu and Benirschke 1977; Benirschke et al. 1984).

Ellerman and Morrison-Scott (1951), followed by Haltenorth (1963) and Roberts (1977) grouped *Gazella bennetti* as a subspecies with *Gazella gazella*. Groves (1969), followed by Lange (1972) and Corbet (1978) placed it with *Gazella dorcas*. Only recently Groves (1985) has revised his views due to the accumulating evidence for an independent position of the Indian gazelle. From the cytological criteria demonstrated above, the investigated animals are too different from both *gazella* and *dorcas* to be interpreted as being just a variation of the karyotype of one of these species. As has been shown, the closest accordance exists with *Gazella subgutturosa*. This is surprising only if this species is really regarded as belonging to a different subgenus (*Trachelocele* Ellerman and Morrison-Scott, 1951). The existence of a throat-swelling in males of the goitred gazelle during the breeding season – which is the character used by Ellerman and Morrison-Scott (1951) to define this subgenus – does not appear to be a good character for a subgeneric separation of *Gazella subgutturosa*. In any case, the remaining cytological differences such as the number of necessary Robertsonian fissions or fusions and the previously unreported form of the Y1 chromosome make it unlikely that our *Gazella bennetti* is too closely related even to the latter species. The karyological differences point to the necessity of establishing *Gazella bennetti* as a species in its own rights. Since *Gazella bennetti* and *Gazella subgutturosa* have an overlap in distribution and since there are no intergrading populations, there would be no doubt that they are separate species even without evidence of karyological differences.

Gazella bennetti was included into *Gazella dorcas* because of similarities in cranial morphology. Having to exclude it now, also changes the range of variation of this last species. Without *bennetti*, the remainder of the Dorcas gazelles becomes more uniform, which in reverse affects the status of other marginal groups. Particularly the other eastern forms with fairly straight horns, like the Saudi gazelle, *Gazella dorcas saudiya* Carruthers and Schwarz, 1935, or Pelzeln's gazelle, *Gazella dorcas pelzelni* Kohle, 1886, are candidates for exclusion from *Gazella dorcas*. Together with the gazelles from the Red Sea islands (Groves 1983) they might rather form a complex with *Gazella bennetti*. It would be interesting to compare the karyotypes of these taxa.

It is obvious from our results that chromosome studies will add further pieces of evidence to the yet uncomplete understanding of evolution and systematics of the gazelles. Future schemes should at any rate separate the forms according to the occurrence of a second Y chromosome in the males, which seems to be a particular evolutionary feature of most gazelles (Wahrman et al. 1973). Thomson's gazelle, and if they are conspecific (Groves 1985) the Red-fronted and Heuglin's gazelle as well, would have to be excluded from the gazelle genus on this basis. Among the gazelles with a double Y chromosome, the subgenus *Nanger* will probably remain a useful subdivision, whereas *Trachelocele* in the sense of Ellerman and Morrison-Scott (1951) will not. It is obvious on morphological grounds that *Gazella subgutturosa* is related to *Gazella leptoceros* (Lange 1972). Our studies have revealed karyological affinities between *subgutturosa* and *bennetti*. Future studies will be necessary to investigate their morphological relations.

Finally, one important remark has to be added: regional aspects must be considered carefully in future chromosome studies of gazelles. As in the case of *Gazella bennetti*, local populations – thought to belong to a more widespread species – may turn out to be independent taxa. It may later be possible to relate karyotypes and geographical distribution. Thus, the geographical origin of the animals under study, even if as unprecise as in our case, must be published together with the karyological results. This is, for example,

not the case in the „Chromosome Atlas" (Hsu and Benirschke 1967/77), from where basic information had to be used in this study as well.

Acknowledgements

The efforts to build up a comparative collection of gazelle skeletons were supported by the "Sonderforschungsbereich 19 – Tübinger Atlas des Vorderen Orients" of the DFG and by the University of Tübingen. We wish to thank these institutions for their support.

Zusammenfassung

Systematik und Chromosomen der Indischen Gazelle, Gazella bennetti (Sykes, 1831)

Bei 3 Individuen von *Gazella bennetti* wurden Chromosomenzahlen von 2n = 50 (♀) und 51 (♂) gezählt. Aufbau und Gestalt der X- und Y1-Chromosomen unterscheiden sich von denen anderer Gazellenarten. Die Indische Gazelle darf nicht als Unterart von *G. gazella* oder *G. dorcas* klassifiziert werden.

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Z. Säugetierkunde 53 (1988) 55–56

ISSN 0044-346

WISSENSCHAFTLICHE KURZMITTEILUNGEN

A note on aquatic and aerial vision in Odontocetes

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Receipt of Ms. 17. 2. 1987

The paper by Neuhaus, which recently (1986) appeared in this journal, contains an over simplified analysis which casts doubt on some of its conclusions. The author presents calculations, based on the anatomy of the eye of the Beluga (White Whale, *Dephinapterus leucas*), from which it appears that the eye is approximately in focus (i.e. well focused on objects at infinity), when it is used under water. Lacking a mechanism for accommodation, it follows that in air, where refraction by the cornea becomes effective, the Beluga must be very near-sighted. This conclusion, however, conflicts with the Beluga's apparent use of vision in air. The author proposes a resolution to this conflict by first assuming that the image formed by the eye under water lies on a flat surface slightly forward of the retina and perpendicular to the optical axis. This paraxial image plane intersects the retina slightly to the side of the optical axis and thus avoids the "blind spot" resulting from the axial location of the optic nerve. Carrying this idea further, the author then reasons that the Beluga could be in focus in air also. That is, as the paraxial image plane moves much closer to the lens, with the addition of the refractive power of the cornea in air, it will again intersect the retina at some greater annular distance from the optical axis. The reader is led to believe that irrespective of the viewing medium or distance the non-focusing eye of the Beluga will be in focus somewhere on the retina (with the underlying assumption that these regions of the retina are capable of good resolution). These ideas were not supported by new data and are inconsistent with a more general geometrical optics analysis. Fundamentally, the assumption that the image is focused on a flat surface is in error and the inferences based on this assumption are also incorrect. Images formed by simple optical systems are projected on a curved surface (which might well be the very reason for the curved shape of the vertebrate retina). This phenomenon is known as the Petzval curvature of the image. For a plane object at infinity and a system of k refracting surfaces, the radius of curvature of the final image in the absence of oblique astigmatism and spherical aberration can be calculated with the following equation (Longhurst 1967, p. 359–360):

$$\frac{1}{R_k} = n_k \sum_{i=1}^{k-1} \frac{1}{r_i} \left(\frac{1}{n_{i+1}} - \frac{1}{n_i}\right),$$

in which R_k is the radius of curvature of the image in the kth medium, r_i is the radius of curvature of the ith refracting surface and n_i is the refraction index after the ith refracting surface. Applying this equation to the eye of the Beluga as described by Neuhaus, for aquatic vision a Petzval curvature of the retinal image is 10.0 mm. In view of the uncertainty of the values used in the calculation, the result may be considered to be in reasonable agreement with the curvature of the retina, which has, according to Neuhaus, a radius of 11.3 mm. We may conclude that the Beluga eye under water is in focus over the entire retinal surface (as could be expected a priori). This near coincidence of the retina and under water image eliminates the need to seek a mechanism to avoid the axially located

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"blind spot" caused by the optic nerve. The other key feature of the NEUHAUS Beluga eye model is that it would be focused in air. However, the aerial Petzval image curvature of the NEUHAUS eye model indicates that the animal is hopelessly near-sighted in air.

One would expect toothed whales to have good far vision in air because echo location does not provide remote sensory information in this medium and good near vision in water because the oceans attenuate light rapidly with distance. In this regard the eye model presented by RIVAMONTE (1976) offers an alternative explanation which agrees with the behaviorally measured near-sightedness in water and far-sightedness in air results of HERMAN et al. (1975). In this model of the eye of the bottle-nosed dolphin *(Tursiops truncatus),* the lens is assumed to be bi-focal, the core having an appreciably higher refractive index than the periphery. The lens core would be primarily functional in aquatic vision, allowing focused near vision under water. By virtue of the peculiar shape of the pupil and location of the lens, in air the image forming light would mainly pass through the less refractive peripheral part of the lens. The combination of a less refractive lens periphery and highly refractive cornea allows focused far vision in air. As argued elsewhere (DRAL 1985), the elements of this model fit nicely into the known facts of ocular anatomy, enhancing its credibility.

Acknowledgements

I am indebted to Dr L. MAAS (NIOZ, Texel) for enlightening me on the computational aspects of this paper, and to Mr. A. RIVAMONTE (Army Primary Standards Laboratory, USA) for his correction of the manuscript.

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Z. Säugetierkunde 53 (1988) 57–58

ISSN 0044-3468

Zur Frage der Sehfähigkeit von *Delphinapterus leucas* in Wasser und in Luft

Von W. NEUHAUS

Eingang des Ms. 25. 8. 1987

In seiner Mitteilung über das Sehen der Zahnwale in Wasser und Luft weist A. DRAL (1987) darauf hin, daß meine Berechnung über das Sehen des Weißwals in Luft, wenn die nach PETZVAL berechnete Bildkrümmung berücksichtigt wird, fehlerhaft wird und zu extremer Kurzsichtigkeit führt. Er selbst vertritt die Auffassung von RIVAMONTE (1976), die eine ganz andere Grundlage als meine Untersuchung hat.

Aus der klaren Zeichnung von PILLERI (1964) konnten die morphologischen Größen des Weißwalauges entnommen werden, die allerdings nicht vollständig mit einigen vom gleichen Autor mitgeteilten Zahlenwerten übereinstimmen (NEUHAUS 1986). Die Brechungsexponenten wurden in Anlehnung an die Verhältnisse des menschlichen Auges erschlossen, der Wert für die Linse jedoch aus den von MATTHIESSEN (1886) gemessenen Brechungsexponenten für die Linse verschiedener Zahnwale und anderer Cetaceen gemittelt. Diese Größe ist 1,60, demnach bis zu einem gewissen Grade willkürlich. Ändert man sie geringfügig auf 1,59, so wird die Brennweite der Linse ein wenig verlängert und die Werte für die Bildkrümmung nach der PETZVAL-Formel verändert. Man erhält dann wie in meiner früheren Untersuchung zwei kreisförmige Zonen scharfen Sehens auf der Retina, eine für das Sehen in Wasser, die andere für das Sehen in Luft (Abb. 1). PILLERI stellte im histologischen Teil seiner Arbeit im Unterschied zu DRAL keine Unterschiede in der Verteilung der Sinneszellen der Retina fest. Die vorstehende Ausführung entspricht bei Berücksichtigung der Korrektur dem Ergebnis meiner früheren Untersuchung.

A. DRAL (1987) vertritt die von C. A. RIVAMONTE (1976) entwickelte Auffassung. Im Wasser ist danach das Auge der Zahnwale bei geöffneter Pupille sehtüchtig. Bewegen sie sich in Luft, so werden die Pupillen wegen der stark gesteigerten Helligkeit bis auf schlitzförmige Öffnungen an den Rändern geschlossen. Das hier einfallende Licht bildet nach der These die Umgebung auf der Retina scharf ab, weil der Brechungsindex und damit die Brechkraft der Linse in den Randbezirken niedriger ist als in der Mitte. Hierdurch soll für das Gesamtauge der Unterschied in den Brechungsindices zwischen Wasser und Luft kompensiert werden.

Der Schichtenaufbau der Linse bringt es bei den Säugetieren mit sich, daß die Brechungsindices allmählich von außen nach innen, und zwar am meisten in den äußeren äquatorialen Schichten (GROTHUISEN 1929) zunehmen.

Bei großer Helligkeit treffen einfallende Lichtbündel allein auf die peripheren Linsenabschnitte mit der stärksten Gradation der Brechkraft. Die Strahlen eines Gegenstandspunktes, z.B. in 2 m Entfernung, divergieren im Auge bis zur Weite der Randschlitze der Pupillen (etwa 0,6–0,8 mm). Die der Linsenmitte näheren Strahlen werden stärker gebrochen als die äußeren, denn die erwähnte Strecke kann bei einem Linsendurchmesser um 6 mm nicht vernachlässigt werden (Abb. 2). Unter diesen Bedingungen kann es nicht zu einer scharfen Abbildung auf der Retina kommen. Auch der verhältnismäßig langsame Pupillenreflex könnte bei den schnellen und oft zentimetergenau gezielten Sprüngen der Delphine für die visuelle Orientierung in Luft (nach RIVAMONTE) hinderlich sein. Die Ausführungen zeigen, daß die von mir vertretene Auffassung über das Sehvermögen des Weißwals in Wasser und Luft aufrechterhalten werden kann.

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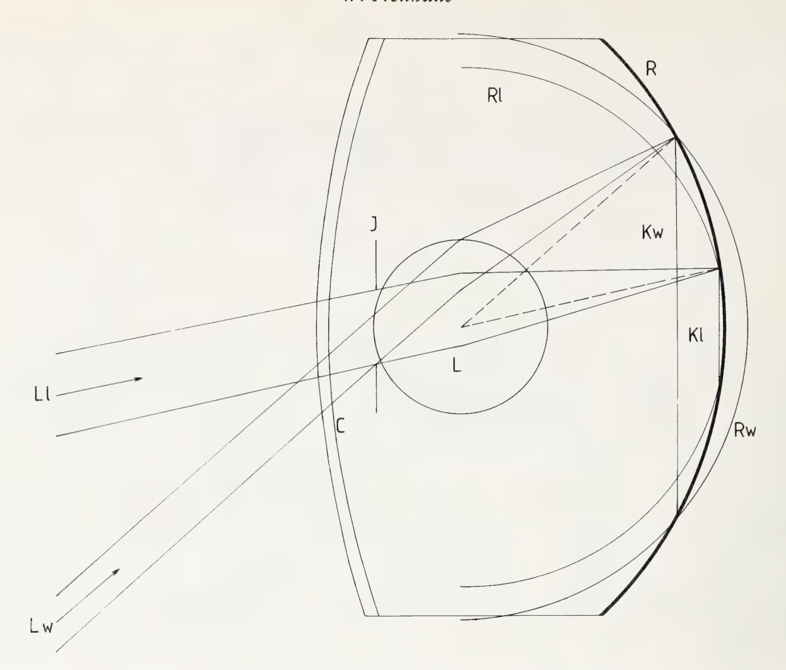


Abb. 1. Schema der Optik des Auges von *Delphinapterus leucas.* C = Cornea, I = Iris, Kw = Projektion der Kreiszone für scharfes Sehen im Wasser, Kl = dasselbe für das Sehen in Luft, L = Linse, Lw = Einstrahlendes Lichtbündel im Wasser, Ll = dasselbe für das Sehen in Luft, Rw = Petzval-Rand in Wasser, Rl = dasselbe in Luft

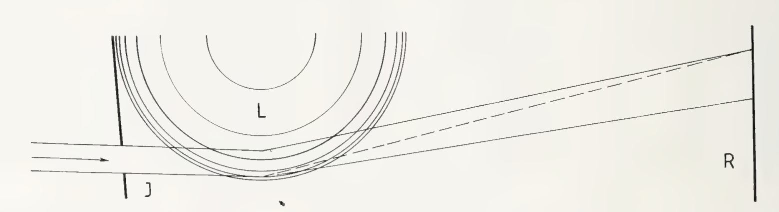


Abb. 2. Schema des Strahlenganges im Auge von *Delphinapterus leucas,* wenn allein Randschlitze der Pupille offen sind. I = Iris (Randschlitz), L = Linse, R = Retina, → einstrahlendes Lichtbündel, - - - hypothetischer Strahl nach der These von Rivamonte

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Z. Säugetierkunde 53 (1988) 59–60

ISSN 0044-3468

On the pupping period of Grey Seals, *Halichoerus grypus* (Fabricius, 1791), reproducing on a shoal near the Island of Terschelling, the Netherlands

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Receipt of Ms. 3. 4. 1987

Although the species must have been common in prehistoric times in view of the many remnants found during excavations, Grey Seals were unknown in the Netherlands until the winter of 1955–56, when a specimen was observed in the vicinity of the Island of Texel (KRISTENSEN 1957). From that winter on many Grey Seals were found on the coast of the Netherlands (HICKLING 1962; VAN HAAFTEN 1974), almost certainly all originating from the large colony in the Farne Islands in the North Sea, opposite the border between England and Scotland. Most of the specimens were very young animals and often in a poor condition. When found these young seals were mostly taken to the Harbour Seals Rehabilitation and Research Centre at Pieterburen, while some were taken to the Nature Education Centre on Texel. After recovery, they were set free again in the North Sea or the adjacent Wadden Sea.

Thus, over the years non-reproducing groups of Grey Seals were formed living in the coastal water of the Netherlands. At present one of these groups is living on and near 'Engelse Hoek', a high lying shoal (53° 20′ N, 5° 10′ E) off the Friesian Island of Terschelling. In the second week of January 1985 pilots of military aircraft reported that they had spotted two female Grey Seals with suckling young. Once this became known, special attention was given to the fact that seals might be born on the shoal. In the last week of January 1986 pilots again reported having seen two females with young. In the first week of February 1987 three newborn Grey Seals were seen lying on the shoal, while 10 days later two more were spotted.

This shoal is a part of the Wadden Sea that remains dry most of the time, being flooded only in case of high northwesterly winds (force 7 de Beaufort and stronger). That is probably the reason why a number of Grey Seals chose this shoal for their habitat. From 1980 to 1986 a total of 55 stranded Grey Seals were taken into the Pieterburen centre, recovered and set free again on this shoal. From observations we know that at present the shoal accommodates a colony of some 45 Grey Seals.

The two Grey Seals born in January 1985 disappeared after heavy weather. One was probably found on the Friesian coast and could be rehabilitated in the Pieterburen centre. The two Grey Seal pups born in the last week of January 1986 also suffered bad luck. They disappeared in stormy weather, one being later found dead on the shore of Terschelling.

The Grey Seal pups born in February 1987 numbered five. Three were found on the shore of Terschelling and survived thanks to treatment in the Pieterburen centre. The other two grew up on the shoal.

That Grey Seals should settle and breed in the coastal waters of the Netherlands was to be expected, but that the pupping period would be in the second and third week of February came as a surprise. After all, the breeding season of the colony of Grey Seals in the Farne Islands, where most of the Dutch specimen come from, starts around the middle of October and lasts until around the middle of December, with a peak by 7 November

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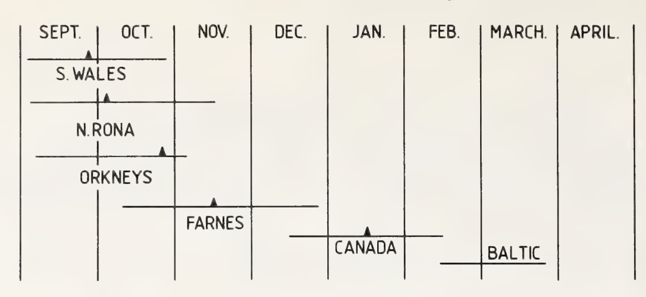


Fig. 1. Pupping seasons and peak times of some Grey Seal colonies. After King (1983)

(Hewer 1974; King 1983). That in the first year Grey Seals had pups on the shoal near the Island of Terschelling in January could be explained by the fact that this involved young females. Young Grey Seals have been known to give birth in the spring (Backhouse and Hewer 1957). That the young near Terschelling should be born in a later period in 1986 and 1987, however, was completely unexpected.

The pupping season of the Grey Seals in the Netherlands looks more like that of *Halichoerus grypus* in the Baltic (Fig. 1). In this short article we will not try and furnish an explanation of the phenomenon, but we only want to draw attention to it in order that it may be studied in the coming years.

To conclude this note, we would like to express our gratefulness for the information we received from pilots of Leeuwarden AFB, and from Mr. Hessel Wiegman.

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Authors' address: Drs Albert Moesker, Zeehondencrêche, Hoofdstraat 94a, NL-9968 AG Pieterburen, The Netherlands

Einladung

Die 62. Hauptversammlung der Deutschen Gesellschaft für Säugetierkunde e.V. findet von Sonntag, dem 2. Oktober, bis Donnerstag, dem 6. Oktober 1988, in Münster statt.

Vorläufiges Programm

Sonntag, 2. Oktober:		Anreise
	19.00 Uhr:	Zwangloser Begrüßungsabend im Zoo-Restaurant (Sentruper Straße)
Montag, 3. Oktober:	9.00 Uhr:	Begrüßung und Eröffnung der Tagung durch den 1. Vorsitzenden im Vortragssaal des Westf. Museums für Naturkunde, Sentruper Straße 285
	9.30 Uhr:	Hauptvortrag zu dem Schwerpunkt „Ethologie", anschließend Kurzvorträge und Poster-Demonstration
	17.00 Uhr:	Mitgliederversammlung
	19.00 Uhr:	Gemeinsames Abendessen im Museum
Dienstag, 4. Oktober:	9.00 Uhr:	Hauptvortrag zu dem Schwerpunkt „Energiehaushalt", anschließend Kurzvorträge
	14.00 Uhr:	Hauptvortrag und Kurzreferate zu dem Schwerpunkt „Verbreitung"
	19.00 Uhr:	Filmabend
Mittwoch, 5. Oktober:	9.00 Uhr:	Diskussionsrunde „Der Artenschutz und die Gesetze"
	14.00 Uhr:	Kurzvorträge, Führung durch den Zoo (Dr. G. Ruempler und Dr. K. Kaiser)
Donnerstag, 6. Oktober:		Exkursion durch das westliche Münsterland (Feuchtwiesen, „Wildpferde", Wasserschlösser)

Alle Interessenten sind zu der Tagung herzlich eingeladen. Neben den angeführten Schwerpunkten werden wir auch diesmal wieder der Vielfalt der säugetierkundlichen Arbeitsgebiete Rechnung tragen (Kurzreferate und Poster-Demonstrationen).

Das Programm mit der Vortragsfolge wird allen Mitgliedern und auf Anfrage auch Nicht-Mitgliedern rechtzeitig vor der Tagung zugesandt. Falls besondere persönliche Einladungen gewünscht werden, wird gebeten, sich an den 1. Vorsitzenden Prof. Dr. E. Kulzer, Institut für Biologie III, Auf der Morgenstelle 28, D-7400 Tübingen, zu wenden.

Bitte melden Sie die Vorträge, die nicht länger als 15 Minuten dauern sollen, und Poster-Demonstrationen für diese Tagung möglichst frühzeitig, spätestens aber bis zum 30. April 1988 beim Geschäftsführer der Gesellschaft, Prof. Dr. U. Schmidt, Zoologisches Institut, Poppelsdorfer Schloß, D-5300 Bonn 1, an.

Fragen zum Tagungsort und zur Organisation sind zu richten an: Dr. M. Berger, Westf. Museum für Naturkunde, Sentruper Str. 285, D-4400 Münster, Tel. 02 51/8 20 84.

Ausschreibung des Förderpreises der Deutschen Gesellschaft für Säugetierkunde 1988

Die Deutsche Gesellschaft für Säugetierkunde schreibt den Förderpreis in Höhe von 3000,– DM als Anerkennung für hervorragende wissenschaftliche Leistungen junger Forscher aus.

Voraussetzung ist eine im Druck vorliegende Arbeit aus den Gebieten Phylogenie und Systematik, Verbreitung, Ethologie, Ökologie und Populationsbiologie der Säugetiere. Die Arbeit muß in den drei vorausgehenden Kalenderjahren erschienen sein. Autoren dürfen nicht älter als 33 Jahre sein.

Bewerbungen oder Vorschläge für den Förderpreis sind zu richten an die Geschäftsstelle der Deutschen Gesellschaft für Säugetierkunde, Prof. Dr. Uwe Schmidt, Zoologisches Institut, Poppelsdorfer Schloß, D-5300 Bonn 1, unter Beifügung von 5 Sonderdrucken.

Der Jury gehören Wissenschaftler verschiedener Hochschulen und Universitäten und Mitglieder der Gesellschaft an.

Der Preis wird bei der Eröffnung der Jahresversammlung der Gesellschaft in Münster (2. 10.–6. 10. 1988) überreicht.

Internationale Kommission für Zoologische Nomenklatur

The following Opinion has been published by the International Commission on Zoological Nomenclature in the Bulletin of Zoological Nomenclature,

vol. 43, part 4 on 11 December 1986:

Opinion No.

1419 (p. 328) *Democricetodon* Fahlbusch, 1964 (Mammalia, Rodentia): *Democricetodon crassus* Freudenthal, 1969 designated as type species.

BUCHBESPRECHUNGEN

Kress, A.; Millian, J.: **The Female Genital Tract of the Shrew *Crocidura russula.*** Advances in Anatomy, Embryology and Cell Biology. Vol. 101. Berlin-Heidelberg-London-Paris-Tokyo: Springer 1987. 76 pp., 31 figs. DM 63,–. ISBN 3-540-16942-3

Die Abhandlung bietet eine umfassende und sorgfältige Dokumentation des weiblichen Genitaltraktes der Haus-Spitzmaus, *Crocidura russula* im elektronenoptischen Bereich. Der Untersuchung liegen Befunde an 38 Individuen zugrunde, die durch Einzelbeispiele *(Neomys, Sorex, Suncus)* ergänzt werden. Die feinstrukturellen Befunde an Bursa ovarica, Tuben, Uterus, Epoophoron, Cervix uteri und Vagina werden unter Berücksichtigung funktionellen und strukturellen Wandels (saisonal, Periode des Sexualcyclus) dargestellt. Damit liegt eine geschlossene Bearbeitung der Feinstrukturen des weiblichen Genitaltraktes für einen Insectivoren vor. Ausgezeichnete EM-Photos erläutern den Text.

Vergleichende Hinweise auf Monotremata, Marsupialia und Chiroptera beschränken sich auf Auswertung des Schrifttums. Eine Reihe von Mißverständnissen, wie etwa die Behauptung „The Marsupials are thought to be the oldest placental mammals", bedürfen der Korrektur, wenn auch die Autorinnen zu dem Schluß kommen, daß die Fortpflanzungsmechanismen der Beuteltiere keineswegs einfacher sind als die der Eutheria und einen alternativen Modus darstellen. Dies ist nicht neu. Unglücklich ist auch die Formulierung, mit der die Soricidae den „more recent species" gegenübergestellt werden. Das Vorkommen von Plesiomorphien ist kein Beweis für direkte Abstammungsverwandtschaft. Der Wert der eigenen Befunde wird durch diese Bemerkungen allerdings nicht beeinträchtigt.

D. Starck, Frankfurt/M.

SCHOPPE, R.: **Die Schlafmäuse (Gliridae) in Niedersachsen.** Lebensraum und Verbreitung von Siebenschläfer, Gartenschläfer und Haselmaus. Naturschutz und Landschaftspflege in Niedersachsen, Beiheft, Heft 14. Hannover 1986. 52 S. DM 7,–.
ISBN 3-922321-36-4

Verbreitung und Lebensraum von Siebenschläfer, Gartenschläfer und Haselmaus in Niedersachsen werden aufgrund von 575 Funden (247 neu, 328 aus der Literatur) beschrieben. 65 % der Angaben betreffen *Glis*, 13 % *Eliomys* und 22 % *Muscardinus*. Für jede Art wird die Verteilung auf zwei Rasterkarten (Rastergröße 25 km^2) dargestellt, einmal nach der Fundzeit und dann nach der Fundzahl abgestuft. Außerdem werden Höhenverbreitung, Habitat und Exposition des Standorts geschildert. Typische Lebensräume werden in guten Fotos illustriert. Schließlich wird die Frage diskutiert, wie weit Konkurrenz zwischen den drei Arten ihre Verbreitung beeinflußt.

Alle drei Schlafmäuse sind auf die Osthälfte Niedersachsens beschränkt. Ihre Nordgrenze verschiebt sich in der Reihenfolge Haselmaus, Siebenschläfer und Gartenschläfer nach Süden. Seit TENIUS (1958) ist dies die erste umfassendere Darstellung der Verbreitung der Schläfer in Niedersachsen und die erste gründliche Kartierung überhaupt. Bemerkenswert ist besonders, daß die Haselmaus offenbar im ganzen westlichen Niedersachsen fehlt, ferner die Vorliebe des Gartenschläfers für Fichten in reinen und gemischten Beständen. Die Arbeit ist gründlich und auch in der Form ansprechend, doch wären eine noch ausführlichere Darstellung der neuen Befunde zu wünschen, wogegen manche Verallgemeinerung entbehrlich ist. So sollten die Aussetzungen des Siebenschläfers auf den Karten ebenfalls hervorgehoben werden. Neue Feststellungen sollten bezüglich ihrer Zuverlässigkeit (Sammlungsexemplar, Nistkastenkontrolle oder bloße Sichtbeobachtung) behandelt werden, damit sie sich kritisch würdigen lassen.

Zu den unzulässigen Verallgemeinerungen gehört, daß Haselmäuse immer in die Bodenvegetation flüchten (S. 24), denn nach ZIPPELIUS und GOETHE (1951) klettern sie bei Störung stets aufwärts. Auch bauen sie nicht als einzige Schläfer freistehende Nester (S. 24), sondern auch Siebenschläfer (z. B. BAUER 1960) und Gartenschläfer (z. B. KAHMANN und THOMS 1974) können dies tun, und bei Bonn fand ich zumindest mehrfach vom Gartenschläfer überbaute und zum Teil als Wochenstube genutzte Amselnester. Im Rheintal schließen sich Sieben- und Gartenschläfer weniger wegen unterschiedlicher Habitatnutzung aus (entgegen S. 43). Vielmehr gibt es hier über weite Strecken rechts nur Sieben-, links nur Gartenschläfer bei ähnlichen Lebensräumen. Die Schlafmäuse sind in Ökologie und Verhalten viel variabler, als regional begrenzte Befunde vermuten lassen. Gerade deshalb sind gründliche Untersuchungen wie die vorliegende wichtig und nützlich. J. NIETHAMMER, Bonn

KUHN, H.-J.; ZELLER, U. (eds.): **Morphogenesis of the Mammalian skull.** Mammalia depicta Vol. 13. Hamburg, Berlin: Paul Parey 1987. 144 pp., 68 figs., 5 tables. DM 80,–.
ISBN 3-490-17718-5

Der vorliegende Sammelband enthält 7 Beiträge zur Morphogenese des Säugerschädels, die auf dem 7. Europäischen Anatomen-Kongreß 1984 in Innsbruck das Thema einer speziellen Veranstaltung bildeten. Sie sind in ihrer Gesamtheit ein eindrucksvolles Dokument für das neu erwachte Interesse an vergleichend-anatomischer Forschung und belegen die Ergebnisse, die in der Morphologie in den letzten Jahren erreicht wurden.

KUHN bespricht in einer synthetischen Einleitung unter Berücksichtigung morphologischer, ontogenetischer, paläontologischer und funktioneller Gesichtspunkte alle jene Probleme, die sich aus dem Wandel vom Schädel der Reptilien zu dem der Säugetiere (Monotremata und Theria) ergeben (Kiefergelenks-/Gehörknöchelchenproblem, Natur und Herkunft der einzelnen Skelettelemente, Exo-Endoskelett, Sekundärknorpel, Ohrkapsel, Seitenwandbildung und Aufbau eines Syncraniums) in knapper und überzeugender Form. ZELLER behandelt als Beispiel für einen basalen Eutherier eine geschlossene Serie von 26 Embryonal- und einigen Postnatal-Stadien von *Tupaia* und ist damit in der Lage, ein differenziertes Bild vom Ablauf der Entwicklungsprozesse für den ganzen Ontogeneseablauf zu entwerfen und eine Reihe offener Fragen zu klären.

Besonders hervorgehoben sei der Beitrag (KUHN und ZELLER) über das Cavum epiptericum und die Seitenwandbildungen, dem ein reiches Material von *Ornithorhynchus*, *Tachyglossus* und Theria zugrunde liegt. Eine subtile Analyse der Inhaltsgebilde des Cavum epiptericum und des Aufbaus seiner Wand erbrachte eine Fülle neuer Befunde und eine Klärung alter Streitfragen. Nervenverlauf im Cavum und Beteiligung einer Lamina obturans an der Wandbildung sind beiden Monotremengattungen gemeinsam, doch ist *Tachyglossus* im Aufbau der sekundären Seitenwand höher organisiert als das Schnabeltier. Bei den Theria erfolgt die Reduktion der primären Seitenwand und der Aufbau einer sekundären Wand (Alisphenoid) in anderer Weise als bei den Monotremen. Beide Stammeslinien müssen außerordentlich früh eigene stammesgeschichtliche Wege eingeschlagen haben. Die Entwicklungsvorgänge in der Orbitotemporalregion des Craniums zeigen in beiden Gruppen autapomorphen Charakter. Ähnlichkeiten im Endeffekt sind Konvergenzen. Die Arbeit bringt nicht nur Klärung von

Homologien, sondern enthält Hinweise auf funktionelle Zusammenhänge. Der Beitrag von W. Maier bringt gleichfalls eine wichtige Erweiterung unserer Kenntnisse von der Morphogenese der Schädelseitenwand. Eine Reihe von 7 Stadien von *Monodelphis domestica* (Marsupialia, Didelphidae), ergänzt durch weitere Beuteltier-Arten, erweitert den Kenntnisstand wesentlich, auch in Hinsicht auf konstruktive und funktionelle Aspekte.

Das Cavum epiptericum entsteht primär nicht als Folge der Hirnvergrößerung, denn es beherbergt bei *Monodelphis* in den Frühstadien ein riesiges Trigeminusganglion. Die Hirnentfaltung erfolgt erst in einer späteren Phase. Schliemann gibt anhand eines umfangreichen Materials von Entwicklungsstadien fissipeder Carnivoren eine vergleichende Analyse der Knorpelstrukturen des Solum nasi, eines für die Phylogenie der Mammalia wichtigen Merkmalskomplexes. Klima berichtet über die Morphogenese des Nasenskelettes der Zahnwale (41 Embryonalstadien, 6 Species) und führt für die meisten Strukturen des Chondrocraniums einen Vergleich mit der Nase terrestrischer Säuger zu einem überzeugenden Resultat.

Der abschließende Beitrag von D. A. N. Hoyte behandelt das alte Problem der Beeinflussung der Schädelform und über diese Hirnform und Hirngröße durch Wirkung der Kaumuskulatur. Untersucht wurden mit Hilfe der Alizarin-Rot-Methode Wachstumsstadien von Kaninchen, Ratte, Meerschweinchen und Schwein. Die Verteilung von Resorptions- und Appositionszonen konnte nicht mit der Wirkung der Muskeln eindeutig in Zusammenhang gebracht werden. Den ontogenetischen Formwandel vom kugligen zum gestreckten Neurocranium führt der Autor hingegen zum Teil auf Muskelwirkung zurück und vermutet auch eine Beeinflussung von Hirnform und Hirngröße.

Die Ausstattung des Bandes ist von hervorragender Qualität. Die Gesamtheit der Beiträge bietet eine gute und koordinierte Übersicht über moderne Probleme der Craniologie und dürfte für Morphologen, Embryologen, Paläontologen und Systematiker unentbehrlich sein.

D. Starck, Frankfurt/M.

Begon, M.; Harper, J. L.; Townsend, C. R.: **Ecology.** Oxford: Blackwell Scientific Publications 1986. 888 pp., 476 ill. £ 14,50. ISBN 0-632-01339-7

Der Inhalt des Buches ist nur richtig einzuschätzen, wenn man den Untertitel kennt: Individuen, Populationen und Gemeinschaften. Die 3 Autoren mit ihren unterschiedlichen wissenschaftlichen Schwerpunkten brachten sowohl die Zoologie als auch die Botanik ein. Sie bauen auf den Eigenschaften der Individuen auf, die im Lichte ihrer Eignung für das Überleben im Lebensraum gesehen werden. Die Ebene der Population wird schwerpunktartig berücksichtigt und die Struktur des Ökosystems unter den Gesichtspunkten der Produktion, des Stofftransports und der Artenkoexistenz behandelt. Die beiden Kapitel „Prädation" und „Ökosysteme" beherrschen das Buch. Es zeichnet sich durch seine „Materialsammlung", die Abbildungen, aus: In 22 Kapiteln bietet es 488 Abb. an; viele aus Originalarbeiten entnommen, andere geschickt entwickelt. Das Durcharbeiten des umgangreichen Bandes wird erleichtert durch „Randmarken", die gleichsam eine Annotierung darstellen. Der Insider findet sich leichter zurecht, für den Studenten bieten sie eine Möglichkeit, sein Wissen autodidaktisch zu überprüfen. Die Randmarkierungen sind außerdem auch deshalb notwendig, weil das Inhaltsverzeichnis zu wenig detailliert ausgefallen ist. Mit rund 900 Zitaten bildet das Literaturverzeichnis eine fundierte Grundlage. Den Umfang verdankt das Lehrbuch seiner Zielsetzung, nämlich sowohl theoretische Grundlagen zu bieten als auch die Ergebnisse von Felduntersuchungen darzustellen und anschließend in einer breiten kritischen Diskussion zu beleuchten.

Wegen seines Aufbaus und seiner Aktualität kann das Lehrbuch sowohl für die Lehre als auch für das Studium uneingeschränkt empfohlen werden. R. Schöpfer, Osnabrück

Regös, J.: **Die grüne Hölle – ein bedrohtes Paradies.** Bericht aus dem Regenwald. Hamburg und Berlin: Paul Parey 1987. 130 S., 158 Abb. DM 39,80. ISBN 3-490-23018-3

Das vorliegende Buch ist das Ergebnis mehrerer Reisen des Verfassers in die Urwaldgebiete Mittel- und Südamerikas. In einer mit unzähligen biologischen Fakten angereicherten, gut bebilderten Reiseschilderung berichtet er über die ungeheure Formenvielfalt und Komplexität der Lebensgemeinschaft Regenurwald, bevor er im 2. Teil des Buches auf die aktuelle Bedrohung des Ökosystems Regenwald durch den Menschen und auf die Auswirkungen der Zerstörung dieses Ökosystems auf den Gesamtwasserhaushalt und die Großklimalage eingeht. Die Waldzerstörung hat zwei Ursachen: Die Bevölkerungsexplosion und großflächige Rodungen durch internationale Konzerne. Als Alternative für eine umweltschonende Regenwaldnutzung empfiehlt der Verfasser hier neben dem sinnvollen Einsatz von Kunstdünger einen Saatwechsel und Multistrata-Produktionssysteme. J. Lange, Berlin



Erscheinungsweise und Bezugspreis 1988: 6 Hefte bilden einen Band. Jahresabonnement Inland: 308,– DM zuzüglich 13,80 DM Versandkosten, Gesamtpreis 321,80 DM einschließlich 7 % Mehrwertsteuer. Jahresabonnement Ausland: 308,– DM zuzüglich 18,– DM Versandkosten. Das Abonnement wird zum Jahresanfang berechnet und zur Zahlung fällig. Es verlängert sich stillschweigend, wenn nicht spätestens am 15. November eine Abbestellung im Verlag vorliegt. Die Zeitschrift kann bei jeder Buchhandlung oder bei der Verlagsbuchhandlung Paul Parey, Spitalerstraße 12, D-2000 Hamburg 1, bestellt werden. Die Mitglieder der „Deutschen Gesellschaft für Säugetierkunde" erhalten die Zeitschrift unberechnet im Rahmen des Mitgliedsbeitrages.

Z. Säugetierkunde 53 (1988) 1, 1–64


PAUL
PAREY


Wolf-Eberhard Barth
Praktischer Umwelt- und Naturschutz
Paul Parey

(2), 65–128, April 1988 ISSN 0044-3468 C 21274 F

ZEITSCHRIFT FÜR SÄUGETIERKUNDE

INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Organ der Deutschen Gesellschaft für Säugetierkunde



Verlag Paul Parey Hamburg und Berlin

This journal is covered by Biosciences Information Service of Biological Abstracts, and by Current Contents (Series Agriculture, Biology, and Environmental Sciences) of Institute for Scientific Information

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Die Zeitschrift für Säugetierkunde veröffentlicht Originalarbeiten und wissenschaftliche Kurzmitteilungen aus dem Gesamtgebiet der Säugetierkunde, Besprechungen der wichtigsten internationalen Literatur sowie die Bekanntmachungen der Deutschen Gesellschaft für Säugetierkunde. Verantwortlicher Schriftleiter im Sinne des Hamburgischen Pressegesetzes ist Prof. Dr. Harald Schliemann.

Zusätzlich erscheint einmal im Jahr ein Heft mit den Abstracts der Vorträge, die auf der jeweiligen Hauptversammlung der Deutschen Gesellschaft für Säugetierkunde gehalten werden. Sie werden als Supplement dem betreffenden Jahrgang der Zeitschrift zugeordnet. Verantwortlich für ihren Inhalt sind ausschließlich die Autoren der Abstracts.

Manuskripte: Manuskriptsendungen sind zu richten an die Schriftleitung, z. Hd. Prof. Dr. Dieter Kruska, Institut für Haustierkunde, Biologie-Zentrum, Neue Universität, Olshausenstr. 40–60, D-2300 Kiel. Für die Publikation vorgesehene Manuskripte sollen gemäß den „Redaktionellen Richtlinien“ abgefaßt werden. In ihnen finden sich weitere Hinweise zur Annahme von Manuskripten, Bedingungen für die Veröffentlichung und die Drucklegung, ferner Richtlinien für die Abfassung eines Abstracts und eine Korrekturzeichentabelle. Die Richtlinien sind auf Anfrage bei der Schriftleitung und dem Verlag erhältlich.

Sonderdrucke: Anstelle einer Unkostenvergütung erhalten die Verfasser von Originalbeiträgen und Wissenschaftlichen Kurzmitteilungen 50 unberechnete Sonderdrucke. Mehrbedarf steht gegen Berechnung zur Verfügung, jedoch muß die Bestellung spätestens mit der Rücksendung der Korrekturfahnen erfolgen.

Mit einer Beilage des Verlages Paul Parey

Fortsetzung 3. Umschlagseite

Verlag: Paul Parey, Hamburg und Berlin. Anschriften: Spitalerstr. 12, D-2000 Hamburg 1; Lindenstr. 44–47, D-1000 Berlin 61. – Printed in Germany by Westholsteinische Verlagsdruckerei Boyens & Co., D-2240 Heide/Holst.

Z. Säugetierkunde 53 (1988) 65–68

ISSN 0044-3468

Sonar used by flying Lesser horseshoe bats, *Rhinolophus hipposideros* (Bechstein, 1800) (Rhinolophidae, Chiroptera), in hunting habitats

By I. Ahlén

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Receipt of Ms. 21. 1. 1987

Abstract

Flying lesser horseshoe bats were recorded in their natural hunting habitats at a number of different localities in Spain. The common sonar pulse consisted of about a 50 ms long CF-signal with a short upward sweep at the start and a downward sweep at the end. The CF-portion of the pulse had its strongest component at about 110 kHz. This is the second harmonic while there is a weaker first harmonic at about 55 kHz. The pulses were repeated about ten times per second. The material did not show much variation which suggests that the auditory system is sharply tuned to the optimal frequency and that the local populations do not show much acoustic variation. One observation indicated that the lesser horseshoe bat might hunt from a perch like a flycatcher.

Introduction

Since the studies of ultrasonic emissions of the lesser horseshoe bat by Kay and Pickvance (1963) the sonar of this species has been known only in general terms. Good sonar data from hunting situations in natural habitats have not been published. From other species we know that there may be important differences between sonar used indoors and outdoors; in outdoor flight the pulses are more developed in shape and specificity than in indoor flight (Ahlén 1981). Is the small variation in frequency described by Kay and Pickvance (1963) for bats flying indoors still valid in a variety of natural field situations? Lesser horseshoe bats are considered to have the highest frequency of all European bats, but are the constant frequency signals pure tones or are there harmonics?

Material and methods

The ultrasonic sonar emitted by lesser horseshoe bats, *Rhinolophus hipposideros* was recorded on a number of different geographical localities in Spain 1982, 1985 and 1986. The bats were recorded when found in the hunting habitats in the surroundings of their roosts. The recordings were 1982 made with a prototype to the D-920 frequency dividing detector (Ahlén et al. 1984) and a cassette recorder. In 1985 recordings were made with a further developed version of the same detector, called D-940. In addition to using cassette recorders, high frequency signals were also recorded with a Racal Store 4 D instrumentation tape recorder. In 1986 most recordings were done with the detector version D-960 which contains a 'time expansion' unit (signals stored in a digital memory and read to the recorder in one tenth of the original speed) (Pettersson 1986). In 1986 visual observations were made with the aid of an image amplifier, Wild Heerbrugg Big2.

Analyses were made of a selection of recordings from Sevilla (Andalusia), Leon (Leon), Oviedo (Asturias), Huesca (Aragon) and Barcelona (Catalonia) provinces (regions) of Spain. The signals were inspected and measured by the use of a digital memory oscilloscope, an FFT-analyser and by making sonagrams.

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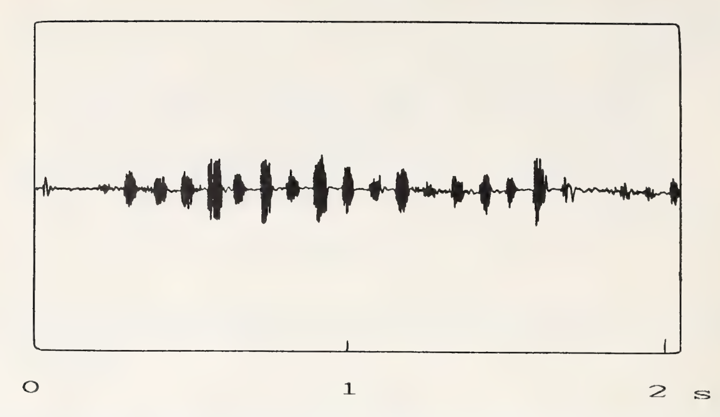


Fig. 1. A pulse train from a lesser horseshoe bat *Rh. hipposideros* flying past the observer shown as an oscillogram (relative amplitude against time)

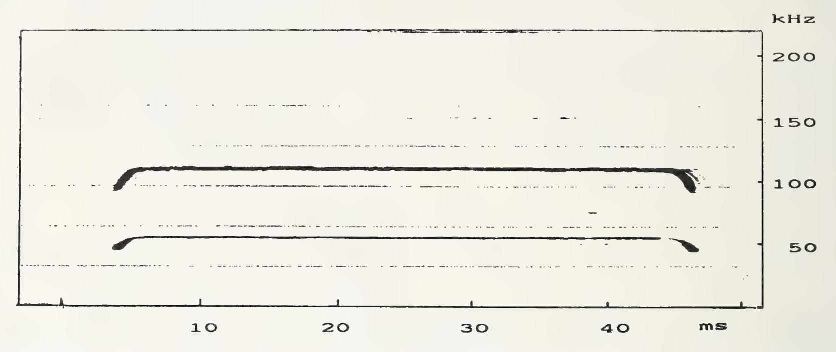


Fig. 2. A single sonar pulse shown as a sonagram with frequency against time. A weak first harmonic at 54 kHz and a strong second harmonic at 108 kHz

Results

The lesser horseshoe bats were found hunting along hillsides or steep cliffs, in small open spaces in scrubland and along low tree galleries at the edge of streams and ponds. Flying bats were also observed along walls of big buildings and stonedikes. Its sonar could only be heard at a short distance, with the D-940 (and D-960) only about 10 meters or even less. The most common sonar type used in these environments had remarkably small variation and was easy to distinguish from the two other *Rhinolophus* species (*ferrum-equinum* and *euryale*) occuring in the same areas. The sonar signals consisted of a fast pulse train with about 50 ms long pulses (40–69 ms, average 48 ms, n = 21) repeated regularly with a little less than 100 ms between the start of each pulse (64–99 ms, average 89 ms, n = 19) (Fig. 1). Each pulse consisted of a long constant frequency signal with the strongest component at about 110 kHz (106–111, average 109 kHz, n = 23), a short upward sweep at the start and a corresponding downward sweep at the end stopping at about 90 kHz. The analyses revealed that there is a weaker first harmonic at about 55 kHz, which means that it is the second harmonic which has the most energy (Figs. 2–3). After this discovery I have noticed that the fundamental is easily heard in the field by tuning the heterodyning to 55 kHz. Some analysed pulses also showed a faint third harmonic at about 165 kHz (Fig. 3).

The occurrence of weak fundamentals together with strong second harmonics have been

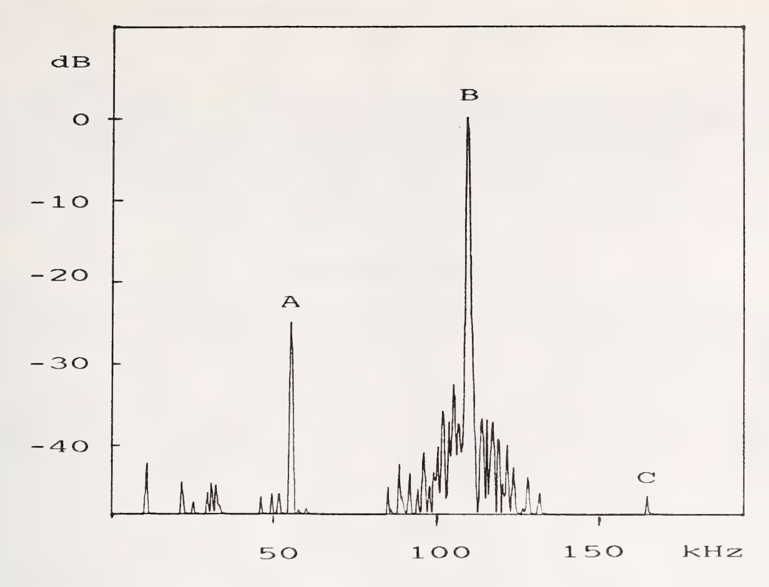


Fig. 3. FFT-analysis (Fast Fourier Transform, with Hanning weighting) of a CF-part of a pulse showing a maximum sound pressure at 110 kHz for the second harmonic (B), a weaker peak at 55 kHz (−42 dB relative to B) for the fundamental (A) and a third harmonic at 165 kHz (C) (−46 dB relative to B)

discussed e.g. by Sales and Pye (1974, p. 58) and was described for *Pteronotus parnellii* (Suga 1984).

The lesser horseshoe bats were also using other sounds at times, especially when they were circling around the entrance to their roosts or when they were hanging on twigs or small rocky outcrops. In the latter cases the differences mainly consisted of a varied pulse length and repetition rate. My material is still insufficient to give a detailed description of these sound types.

At one occasion I made an observation suggesting that *Rh. hipposideros* can use the 'flycatcher' behaviour described in tropical *Rhinolophus* species (Schnitzler et al. 1985). A lesser horseshoe bat was observed hanging on a small rocky outcrop. After a while it flew away out in the vegetation. I could hear it fly around but lost contact with it very soon. Coming back to the rock a couple of minutes later, I found the bat hanging on exactly the same place again.

Discussion

Bats with CF-components can separate their frequencies individually and thus might avoid interference (Miller and Degn 1981). They are likely to return to their optimal frequencies when hunting alone. Rhinolophid bats can compensate for doppler shifts to keep echo within a narrow band of best auditory frequencies (Schnitzler and Henson 1979; Sales and Pye 1974).

The ultrasonic sounds used by *Rhinolophus hipposideros* in a summer nursery colony (indoors) were studied in England by Kay and Pickvance (1963). They reported that the female bats had a very small range of frequencies, only 3 kHz, from 110–114 kHz. The small range of frequencies seems surprising since about 60 bats were present. K.-G. Heller (pers. com.) recorded hand-held specimens of five *Rhinolophus*-species where *Rh.*

hipposideros of various origin (Southern Germany and Greece) ranged from 105 to 111 kHz.

When comparing the same bat species from a number of geographically different localities it could not be excluded that there is a greater variation in frequency. Therefore it is noteworthy that even my data on *Rh. hipposideros* from a number of colonies in different parts of Spain did not show much variation. This suggests that the auditory system is sharply tuned to the optimal frequency of the species and that the local populations do not show much acoustic variation.

Acknowledgements

This study was made possible in 1982 in connection with a study travel financed by the Swedish National Environmental Protection Board, in 1985 with the Spanish state's grants for scientific cooperation between Spain and Sweden and in 1986 with economical support from the Swedish University of Agricultural Sciences.

I thank Dr. L. Miller, Odense, for valuable suggestions when analysing the material and preparing an earlier draft of this article. I also thank Dr. H. Baagøe, Copenhagen, for cooperation in the field work and for critical comments on the manuscript. Finally I thank Dr. K.-G. Heller, Erlangen-Nürnberg, for kindly providing me with results from his sound recordings.

Zusammenfassung

Ortungslaute von fliegenden Kleinen Hufeisennasen, Rhinolophus hipposideros (Bechstein, 1800) (Rhinolophidae, Chiroptera), in Jagdbiotopen

Laute der fliegenden Kleinen Hufeisennasen wurden mit Tonbandgerät in natürlichen Jagdbiotopen in vielen Lokalitäten in Spanien aufgenommen. Der gewöhnlichste Ortungslaut besteht aus einem etwa 50 Millisekunden langen konstantfrequenten Signal mit einem kurzen frequenzmodulierten Anfangs- und Endteil. Der Konstantfrequenzteil hat die stärkste Komponente mit etwa 110 kHz. Das ist der erste Oberton, während der Grundton bei 55 kHz schwächer ist. Die Laute werden etwa zehnmal pro Sekunde ausgesendet. Die Variation an Ortungslauten zwischen Individuen und Populationen war sehr klein, wahrscheinlich ein Ausdruck für einen sehr engen reizbaren Frequenzbereich im Gehörorgan. Eine Observation deutet an, daß Kleine Hufeisennasen die Jagdtechnik der Fliegenschnäpper benutzen.

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Z. Säugetierkunde 53 (1988) 69–75

ISSN 0044-3468

Structure of *Lepus nigricollis* hair from various body regions with Scanning Electron Microscopy

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Receipt of Ms. 21. 1. 1987

Abstract

Scanning Electron Microscopic (SEM) studies were made on the morphology of hair samples of the head, neck, dorsal body, ventral body, fore-limb, hind-limb and tail regions of the Indian hare, *Lepus nigricollis*. The hairs of various body regions tend to differ in colour and size. The type and pattern of arrangement of cuticular scales of these hairs also vary considerably from region to region. Scanning electron microscopic studies on the morphology of hairs of various body regions of any mammalian species form a useful tool in the identification of prey species by the analyses of faecal matter of predators, and for evidences for the presence of various species of animals in any forest habitat.

Introduction

'Trichology', the scientific study of hairs has specific relevance in the dietary investigation of carnivores and field survey of mammals (Day 1966; Dreyer 1966; Ryder 1973; Perrin and Campbell 1979; Keogh 1983; Buys and Keogh 1984). Data obtained from recent wildlife surveys in various forests of Kerala make it possible to determine that there is a need for the identification of various mammalian hairs, especially those of the prey species, which facilitate the conclusive identification of the presence of various mammal hairs in the faeces of predators (Vijayan et al. 1979; Balakrishnan 1984; Balakrishnan and Easa 1986). The faecal matter of most of the wild predators have considerable quanta of hair and occasionally have undigested bones. The hairs of larger prey such as the sambar deer, *Cervus unicolor* and the spotted deer, *Axis axis;* can be comparatively easily identified in the droppings of larger carnivores such as the tiger, *Panthera tigris* and the wild dog, *Cuon alpinus*. However, a thorough identification of hairs commonly seen in the droppings of smaller predators such as the jungle cat, *Felis chaus;* the Asiatic jackal, *Canis aureus* and the Indian fox, *Vulpes bengalensis*, are difficult. Hence, an attempt has been made to identify hairs of a number of mammalian species from various forests of Kerala with the aid of Scanning Electron Microscopy. The present report incorporates the data on the fine structure of hairs of various body regions of the Indian hare, *Lepus nigricollis*.

Material and methods

Lepus nigricollis (Cuvier) of both sexes (four males and four females) were trapped from forest habitats in Wynad and Trivandrum, Kerala and hair samples were plucked carefully from their head, neck, dorsal body, ventral body, fore-limb, hind-limb and tail regions using a fine forceps. These samples were kept in hexane or in 70 % alcohol for 1–72 h for cleaning and were dehydrated in ascending grades of alcohol. Hair samples were cross sectioned at about the middle portion using a fine stainless steel knife. A few hairs were also sectioned longitudinally.

The samples were then mounted on studs, dried using a vacuum dryer and gold coated in a Type JEE 4B Vacuum Evaporator at high vacuum. These samples were scanned under a JOEL JEM 100C/JOEL JSM 35 Scanning Electron Microscope at an accelerating voltage of 10 kV and studied at magnifications ranging from X300 to X10,000. For comparison, exposures from middle portions of the samples were used.

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Results

Observations on the morphology of hair collected from different regions did not reveal any marked sexual dimorphism and hence the data from male and female hares were combined. The table shows the data on size and pattern of colouration of hair samples of various body regions. In general, these hairs have a length of 10–25 mm depending on the body site of its

Table. **Showing the size and colour pattern of hairs of various body regions of the Indian hare, *Lepus nigricollis***

Body region	Hair size, mm*		Colour pattern of hair			
	Minimum	Maximum	Proximal	Middle	Distal	Distal tip
Head	10	12	White-brown	Black	Cream	Black
Neck	18	22	Cream	Grey	Cream	Black
Dorsal body	18	25	White	Black	Cream	Black
Ventral body	12	18	White	White	White	White
Fore-limb	10	12	White	White	Cream	Cream
Hind-limb	15	20	White	Grey	Cream	Black
Tail	16	20	White	Black	Cream	Black

* Data represent a minimum of 30 samples from each region

origin. The differential colour pattern also helps to identify hairs of one region from those of the other. The hairs of ventral body regions are particularly white and smooth, whereas those of other regions have bands of two to four colours such as white, black, cream and grey. The type and pattern of arrangements of cuticular scales of hairs of different body regions observed with the SEM revealed the following:

Head and neck: The cuticular scales of the hairs of head and neck of the hare are flattened, conical-shaped and are tightly packed. There are a number of ridges and grooves on the surface of neck hairs in the longitudinal plane as a result of the pattern of arrangement of the scales (Fig. 1). The pattern of arrangement of the scales could easily be used to distinguish head hair from body regions, but neck hair and fore-limb hair could not be distinguished by scale patterns.

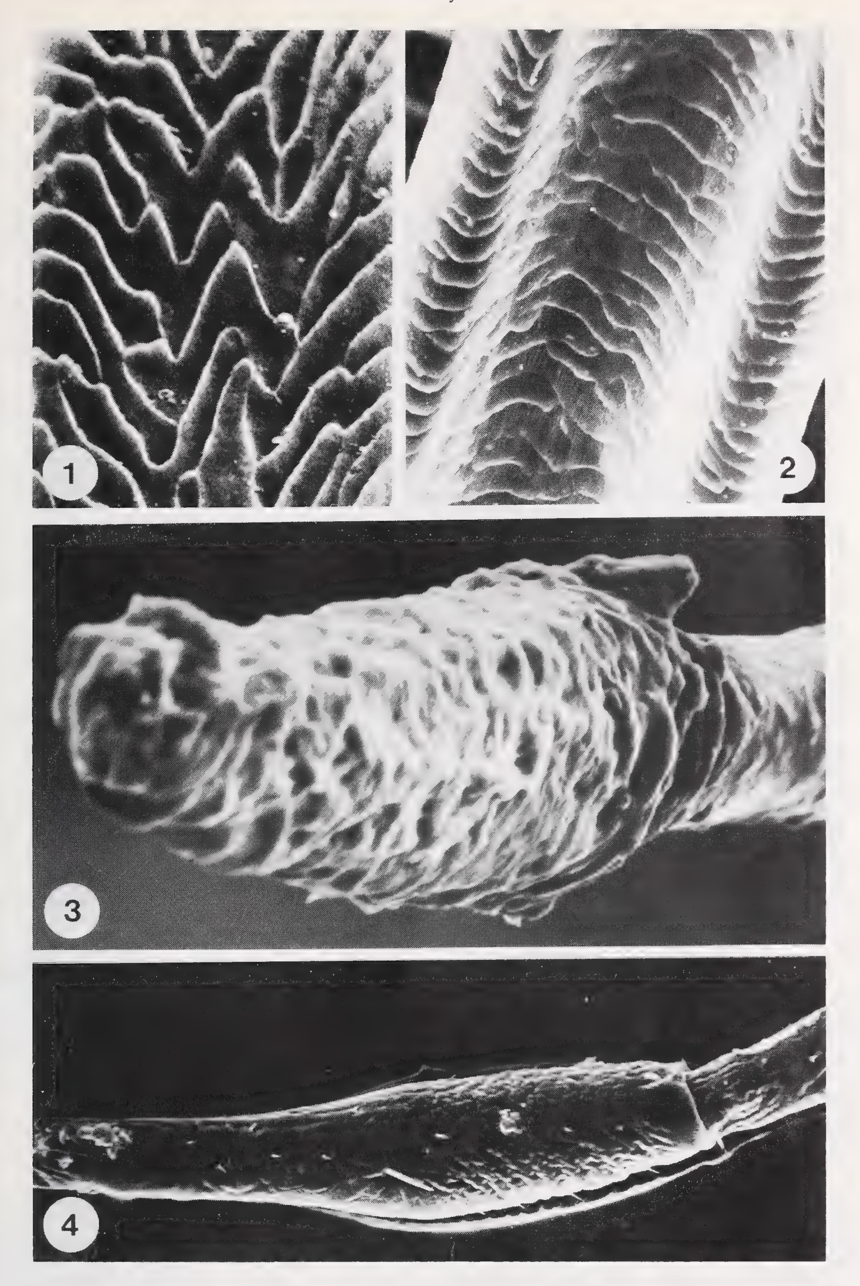
Dorsal body: The cuticular scales of dorsal body hair are flattened and are thickly packed (Fig. 2). Roots of these hairs are thick showing the typical patterns of roots of hare hairs (Fig. 3).

Ventral body: The scales of ventral body hair are elongated in shape and are tightly packed. Elongated grooves on the cuticular surface are also seen as in the case of neck hairs. These hairs are deep-rooted. However, the root is thin (Fig. 4) when compared to the other hair roots. The medulla of these hairs is divided into two columns by the mid-medullary growth of cortical tissues (Fig. 5).

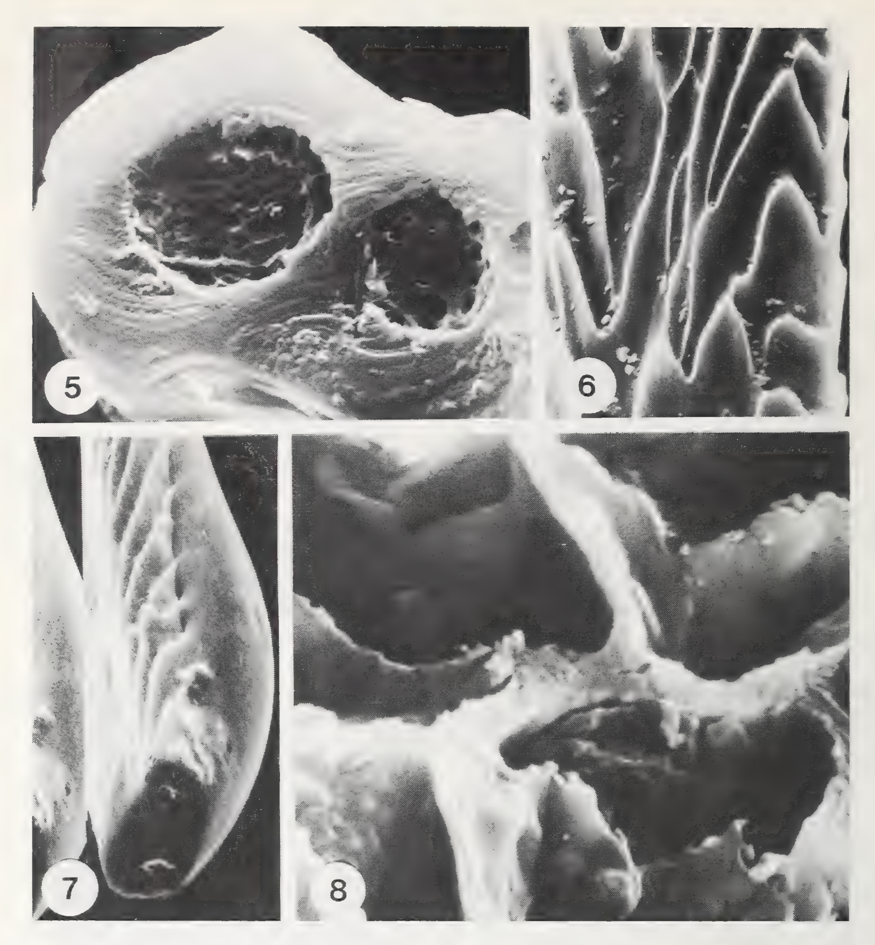
Fore-limb: The scales of the hair of fore-limbs are flattened and elongated, and the distal ends are conical-shaped (Fig. 6). These hairs are not deep-rooted. The proximal portions of them are more or less oval in shape. Cuticular scales are also seen on the surface of these roots (Fig. 7). Well developed medullary cells of these hairs are shown in Fig. 8.

Hind-limb: The scales of the hair of hind-limbs are flattened and thickly packed along the entire length (Fig. 9). The cortex is thin and the medulla is extended with larger cells (Fig. 10).

Tail: The cuticular scales of the hair of the tail are flattened and are similar to scales of hair of the dorsal body region. These scales are also tightly packed in a uniform pattern (Fig. 11).



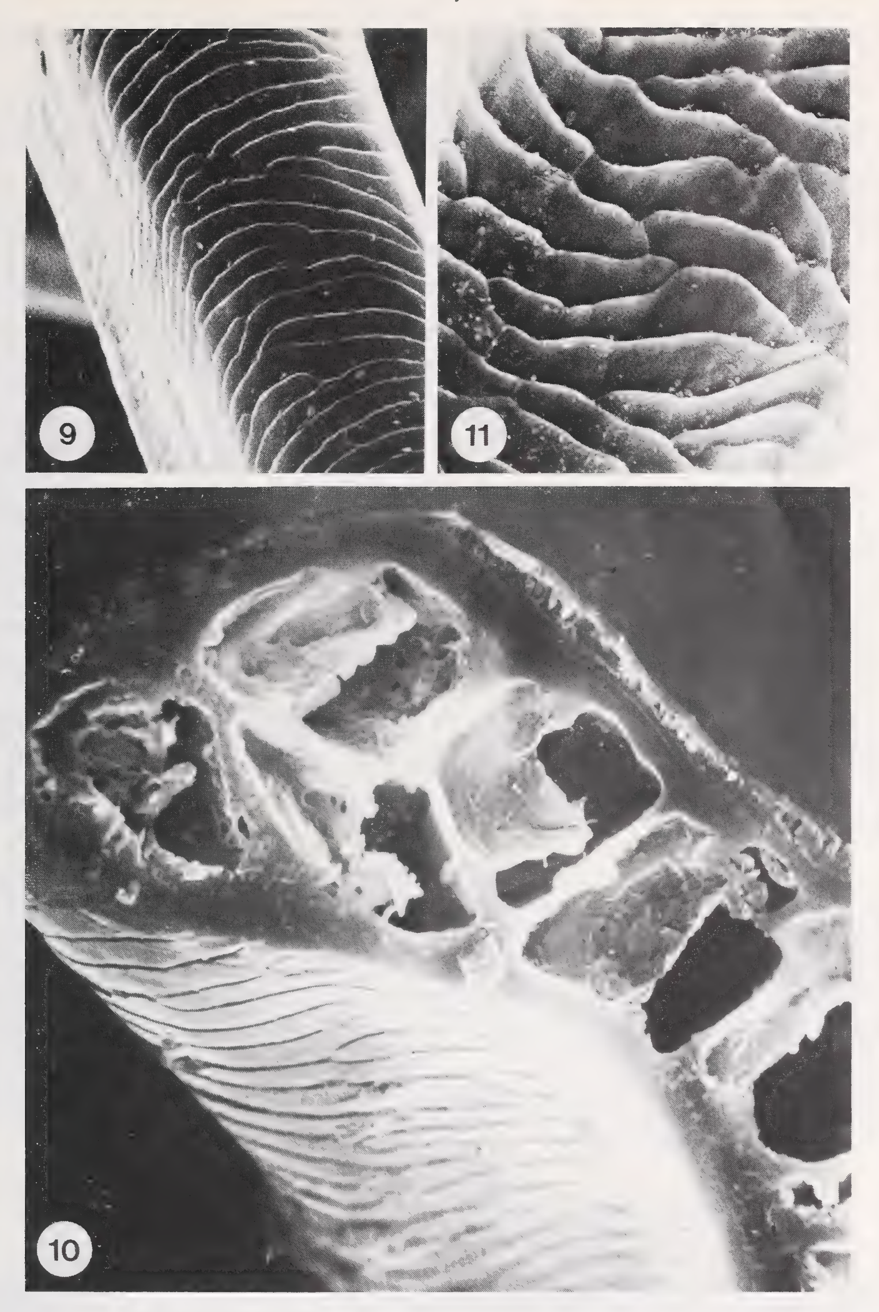
Figs. 1–4. 1: The flattened, elongated and conical shaped cuticular scales of the head and neck hair. (×1,370); *2:* Dorsal body hair showing the tightly packed pattern of arrangement of cuticular scales. (×1,370); *3:* The typical structure of root of hairs of head and dorsal body. (×910); *4:* The morphology of a root of ventral body hair. (Note the difference in the size and shape of roots of dorsal body hairs). (×1,830)



Figs. 5–8. 5: The cross section of a ventral body hair showing the partition of medulla into two columns. (×4,120); *6:* Fore-limb hairs have elongated cuticular scales with conical shaped apices. (×1,280); *7:* The oval shaped roots of fore-limb hairs are shown. Note the development of cuticular scales on roots and the proximal openings of the medulla. (×2,390); *8:* The medullary cells of the fore-limb hair showing the pattern of arrangement of chamber-like formation with the development of intercellular septa. (×4,120)

Discussion

It has been emphasized that identification of ingested hair is a useful tool determining the feeding habits and food preferences of predators (Brunner and Coman 1974; Perrin and Campbell 1979). Identification of hairs may also play a salient role in the field of forensic science (Adorgan and Kolenosky 1969; Keogh 1983). However, only a few mammals have been subjected to systematic studies on the structure of hair (Noback 1951; Lyne and McMahon 1951; Benedict 1957; Stains 1958; Khemelevaskaya 1965; Day 1966; Adorjan and Kolenosky 1969; Trevor-Deutch 1970; Ryder 1973; Brunner and Coman 1974; Koppiker and Sabnis 1976, 1977; Perrin and Campbell 1979; Sokolov 1979; Keogh 1983; Rajaram and Menon 1986). Despite the structural differences of cuticular scales of different species of mammals discernible during these studies



Figs. 9–11. 9: Showing the hind-limb hairs with tightly packed flattened scales. (×1,540); *10:* A cross section of a hind-limb hair showing the pattern of arrangement of medullary cells. (×2,340); *11:* The tail hair with tightly packed, flattened cuticular scales. (×1,180)

(Hashimoto and Shibazaki 1975), major distinguishing features of hairs of different body parts of the same animal were not observed.

The present study made it possible to observe distinguishing features in the types, and in the pattern of arrangement of cuticular scales of hairs of various body regions of *L. nigricollis.* The type and pattern of arrangement of the cuticular scales of hair are found to be prominent factors in differentiating the hair of one region from those of the other. In addition to the patterns of arrangement of cuticular scales of the cortex, the medullary cells also help to differentiate the hair of various body regions. These features can be clearly observed by scanning diverse samples of hair of different body regions, and can depend on these for the identification of hair samples of various species (Rajaram and Menon 1986) as well as hair of different regions of the same species.

Faecal analyses of predators indicate that the droppings have lots of hairs of prey animals. Undigested materials in the faeces of predators would provide information on food preferences of any animal species. Hence identification of hair samples in the droppings of predators would be helpful for studies on the feeding habits of predators. This necessitates a thorough investigation, on the structure of hair samples of various body region of all the prey animals in any forest. Scanning electron microscopic studies on the morphology of the hairs form a comparatively easy and fool-proof technique to identify the hairs of any species. Since the fine surface structure of hair of various body regions of the same animal differ considerably, it is necessary to study the hair samples of various body regions of any species for a knowledge on the structure of body hairs and for detailed analyses of faecal remains of hair samples. Although many of the smaller prey animals could not be seen directly during field surveys (Balakrishnan 1984; Balakrishnan and Easa 1986), the presence of hair in the faeces of predators provides indirect evidence for the presence of these species in the forest area. Further detailed studies on the fine structure of various mammalian hair would be helpful for identification of hair which may be seen on fences, twigs and on the habitat and exploratory grounds of animals. This, in turn would be helpful for species identification and for inferences of animal movements in any forest habitat.

Acknowledgements

Part of this investigation was carried out at the A. N. Severtzov Institute of Evolutionary Animal Morphology and Ecology of the USSR Academy of Sciences, Moscow during the tenure of an Academic Exchange Fellowship Programme of the Indian National Science Academy, New Delhi with the USSR Academy of Sciences, Moscow. I am grateful to Academician V. E. Sokolov and Dr. T. P. Evgenjeva of the above Institute for facilities and for various helps rendered during the period of this investigation. I am also grateful to the Director of the CSIR Regional Research Laboratory, Trivandrum, Mr. Peter Koshy, Scientist-in-charge of the SEM and the technical staff of the Division for providing their facilities to carry out part of this investigation. I am thankful to Prof. K. M. Alexander, University of Kerala for encouragement and for critically reading the manuscript. Financial assistance from the State Committee on Science, Technology and Environment, Government of Kerala is also acknowledged.

Zusammenfassung

Struktur der Haare von Lepus nigricollis aus verschiedenen Körperregionen im rasterelektronenmikroskopischen Bild

Rasterelektronenmikroskopische Untersuchungen wurden an Haaren aus verschiedenen Körperregionen vom indischen Hasen *Lepus nigricollis* durchgeführt. Die Haare dieser Art zeigten regionale Unterschiede in Färbung und Größe sowie in der Ausprägung der Cuticular-Muster. Vergleichbare Untersuchungen an anderen Säugetieren können einen hilfreichen Beitrag zur Artbestimmung an Haaren liefern. Sie sind insbesondere dann von Nutzen, wenn das Beutetierspektrum von Raubtieren über Kotanalysen erfaßt werden soll.

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Z. Säugetierkunde 53 (1988) 76–82

ISSN 0044-3468

Eine jungpleistozäne/altholozäne Nager-Abfolge von Antalya, SW-Anatolien (Mammalia, Rodentia)

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Eingang des Ms. 9. 2. 1987

Abstract

An upper Pleistocene/lower Holocene rodent succession from Antalya, SW Anatolia (Mammalia, Rodentia)

From Middle Paleolithic through Early Upper Paleolithic layers there was an increase of aridity and steppe conditions. While steppe predominated, minor ecological changes may have occurred during the "Epipaleolithic". Obviously, *Microtus gud* was at least locally replaced in the Taurus Mts. by *M. nivalis*, a rather recent western immigrant. *Mus abbotti* and *Meriones tristrami* made their first appearance in uppermost Pleistocene and Holocene layers, respectively. Some species did not survive the upper Pleistocene in the area under study. Nevertheless, a marked ecological and faunal stability becomes evident.

Einleitung

Die beschriebenen Nagerfunde stammen aus der Höhlenstation Karain, etwa 30 km NWN von Antalya an der anatolischen Südküste gelegen. Das Höhlensystem liegt am Rand der riesigen Travertinebene von Antalya in kreidezeitlichem Kalk des Taurus. Der Eingang in 450 m ü. NN überblickt die etwa 150 m tiefer liegende Ebene bis hin zum Meer.

Die Ausgrabungen von Karain B fanden in Zusammenarbeit des Instituts für Urgeschichte der Universität Tübingen mit der Universität Ankara vom 16. Sept.–4. Nov. 1985 statt. Die pleistozänen Sedimente wurden mit einer Maschenweite von 1 mm geschlämmt und vor Ort auf Artefakte und Kleinfauna ausgelesen (Albrecht 1986).

Daten zur jüngeren Kleinsäuger-Faunengeschichte und ihrem klimaökologischen Hintergrund in Anatolien sind außerordentlich dürftig. Das jungpleistozäne/altholozäne Profil von Karain B soll in dieser Hinsicht als ein Mosaikstein dienen.

Ergebnisse und Diskussion

Das jungpleistozäne/altholozäne Nagerprofil von Karain B

Durchlaufende Arten sind *Spalax nehringi, Apodemus mystacinus* und *Microtus guentheri.* Gemeinsam belegen sie offenes, relativ trockenes Gelände sowie nackte Gesteins- und Felspartien. Diese 3 Arten sind gleichermaßen kennzeichnend für die heutigen und die pleistozänen Kleinsäugerfaunen des westlichen Anatolien. Sie kommen im jüngeren Mittelpleistozän (?mittleres Steinheimium) von Chios vor (Storch 1975; Chios war zu dieser Zeit Teil des anatolischen Festlands), *Apodemus mystacinus* und *Spalax* cf. *nehringi* liegen auch schon im Altpleistozän (Altbiharium) von Kalymnos vor (Kuss und Storch 1978; auch die Dodekanes-Insel Kalymnos war zu dieser Zeit Festland).

Die Nager der mittelpaläolithischen, über 30000 Jahre alten Abtragungseinheiten lassen im Ensemble auf relativ günstige Umweltverhältnisse schließen. *Sciurus anomalus* und *Apodemus flavicollis* benötigen Wald, zumindest aber Streifen dichter, höherer Vegetation.

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Tabelle 1. **Das jungpleistozäne/altholozäne Nagerprofil von Karain B, Vilayet Antalya, Türkei**

Abtragungseinheiten	32	31	30	29	28	27	26	25	20	19	18	17	16	13	11	10	9	Rezent
Citellus xanthoprymnus			x	–	–	x	–	x	–	–	–	x	–	–	–	–	–	x
Sciurus anomalus		x									x	–	x	–	–	x	–	x
Myomimus roachi	x	x																?
Spalax nehringi	x	x	x	x	x	x	–	–	x	x	x	x	x	x	x	–	–	x
Mus abbotti												x	x	–	–	–	–	x
Apodemus sylvaticus	x	x	x															x
Apodemus flavicollis	x	x								x								
Appodemus mystacinus	x	x	–	x	x	x	–	–	–	x	x	x	x	–	–	–	–	x
Cricetulus migratorius			x	–	x	–	–	–	x	–	–	–	x	–	–	–	–	x
Mesocricetus brandti			x	x	x	–	–	–	x	x	x	x	x					
Meriones tristrami																x	x	
Microtus guentheri	x	x	x	–	x	x	–	x	x	x	–	x	x	–	–	–	–	x
Microtus arvalis	x	x	x	–	x	x	x			x								
Microtus gud	x	x	x	x	x	x	x	x	x	x	x	x						
Arvicola sp.	x	x	–	x														
Archäologische Datierung	Mittel-		Älteres Jung-				Epi-							Chalkolithikum				
	Paläolithikum																	
	Pleistozän													Holozän				

Heutige Vorkommen nach Besenecker et al. (1972), Corbet und Morris (1967), Felten et al. (1971), Kumerloeve (1975), Osborn (1965) und Storch (1978). *Myomimus roachi* ist nur von der anatolischen W-Küste belegt, jedoch schließen subfossile Nachweise bei Finike, Antalya, ein Überdauern im Untersuchungsgebiet nicht aus.

Für *Microtus arvalis* und *Arvicola* sp. ist im ganzen Jahr verfügbare saftige krautige Vegetation und ausreichende Pflanzendeckung zu fordern. *Microtus gud* ist an zerklüftetes Gestein gebunden und kommt auch im Wald vor, wo dieser nicht völlig geschlossen ist. Gegenüber der nahverwandten und ebenfalls petrophilen Schneemaus, *Microtus nivalis,* ist *M. gud* stärker hygrophil (Spitzenberger 1971; Steiner 1972). Unter Einschluß der im Profil durchlaufenden Offenlandbewohner und von *Myomimus roachi,* der heute steppenartige Lebensräume bevorzugt, zeichnet sich eine recht große ökologische Vielfalt ab.

Im Älteren Jungpaläolithikum etablieren sich mit *Citellus xanthoprymnus* und *Mesocricetus brandti* ausgesprochene Steppenbewohner, und auch das heutige Verbreitungsgebiet von *Cricetulus migratorius* schließt zum größten Teil Steppen ein. *Citellus* und *Cricetulus* leben noch im Untersuchungsgebiet, nicht aber *Mesocricetus brandti,* dessen Verbreitungsschwerpunkt heute im anatolischen Hochland liegt (Spitzenberger 1972). Die Zunahme von Bewohnern offener trockener Lebensräume geht auf Kosten von Arten, die hinsichtlich Feuchtigkeit und Vegetation anspruchsvoller sind. *Apodemus flavicollis* und *Sciurus anomalus* sind im Älteren Jungpaläolithikum nicht belegt, und die Nachweise von *Apodemus sylvaticus, Arvicola* sp. und *Microtus arvalis* enden nacheinander. Es zeichnet sich also eine leichte Verschiebung zu arideren Verhältnissen ab. *Arvicola* verschwindet damit offenbar endgültig aus dem Untersuchungsgebiet, denn der rezente *A. terrestris* ist in Anatolien nur von sehr wenigen Fundpunkten bekannt, die aber nicht den Südwesten einschließen (Osborn 1962).

Im „Epipaläolithikum" müssen großräumig Steppenverhältnisse weiterbestanden haben *(Citellus, Mesocricetus, Cricetulus).* Ab der Abtragungseinheit 20 (C14 Datierung 14160 ± 210 Jahre BP) könnte sich jedoch eine kurzzeitige Verbesserung lokalklimatischer Verhältnisse widerspiegeln: *Apodemus flavicollis* und *Microtus arvalis* sind nochmals nachzuweisen (Abtragungseinheit 19), und *Sciurus* tritt wieder auf (Abtragungseinheit 18). *A. flavicollis* und *M. arvalis* kommen im Untersuchungsgebiet nach diesem Zeitpunkt offensichtlich nicht mehr vor (heutige Verbreitung von *M. arvalis* s. Felten et al. 1971; für *Apodemus* fehlen allerdings neuere Daten). Gegen Ende der „epipaläolithischen" Schichtenfolge scheinen die klima-ökologischen Verhältnisse wieder etwas ungünstiger geworden zu sein. Das kontinuierliche Auftreten von *Microtus gud* über die jungpleistozäne Abfolge endet in Abtragungseinheit 17. Heute ist der nahverwandte *M. nivalis* durch die gesamte Tauruskette bis in den Libanon und Antilibanon südwärts verbreitet, während *M. gud* nur von einem Reliktvorkommen aus dem östlichen Mitteltaurus bekannt ist (Spitzenberger 1971). Dieser Befund spricht dafür, daß *M. nivalis* im Untersuchungsgebiet ein junger Immigrant von Westen her ist. Dort ist er auch schon im jüngeren Mittelpleistozän von Chios belegt (Storch 1975). *M. nivalis* ist weniger hygrophil, was für die zumindest gebietsweise erfolgte Verdrängung des alteingesessenen *M. gud* sicherlich von mitentscheidender Bedeutung war. *Mus abbotti* erscheint im Karain-Profil erstmals gegen Ende der pleistozänen Schichtenfolge. Es ist eine offene und trockene Lebensräume bevorzugende Outdoor-Art der Hausmäuse.

Zwischen der pleistozänen Serie und dem holozänen Schichtpaket ist ein Hiatus von mehreren tausend Jahren anzunehmen. Es gibt, im Gegensatz zu jungpleistozänen Abtragungen, nur Einzelfunde aus dem Altholozän. Auffällig ist dabei, daß sie die frühesten Nachweise von *Meriones tristrami* einschließen (chalkolithische Abtragungseinheiten 10-9). Dieser reine Trockensteppen-Bewohner könnte eine sich im älteren Holozän verschärfende Aridität bezeugen. *M. tristrami* liegt schon im Altpleistozän SW-Anatoliens vor (Kuss und Storch 1978), so daß ihr Fehlen in der jungpleistozänen Abfolge nicht mit „mangelnder Verfügbarkeit", sondern ungeeigneten Lebensbedingungen zu erklären wäre.

Verglichen mit mitteleuropäischen Verhältnissen zeigt das jungpleistozäne/altholozäne Nagerprofil von Karain B erwartungsgemäß weit weniger betonte faunistische Veränderungen. Unter Einschluß älterer Lokalfaunen (Storch 1975; Kuss und Storch 1978) wird

überhaupt eine bemerkenswerte ökologische und faunistische Stabilität im Pleistozän SW-Anatoliens deutlich. Steppen hatten immer eine prägende Rolle gespielt, und nackte zerklüftete Gesteinspartien mußten immer verfügbar gewesen sein. Wälder und Feuchtgebiete unterlagen in ihrer Ausdehnung aber Schwankungen, wie sie auch in der Kleinsäugerfauna des Karain-Profils reflektiert werden. Derzeit erscheint allerdings der Versuch, solche Oszillationen mit den in Mitteleuropa mehr oder weniger etablierten Biozonen parallelisieren zu wollen, wenig sinnvoll.

Bemerkungen zu einzelnen Taxa

Gattung Mus

Mus abbotti Waterhouse, 1837 (= *Mus spicilegus* „Sud" in Orsini et al. 1983): Die von Kratochvíl (1986) herausgearbeiteten Artkriterien an den M1/1 treffen im vorliegenden Material zu. Am M1/ sind t1 und t4 durch eine tiefe Mulde getrennt und treten an der lingualen Kronenkontur als selbständige Höcker hervor. Am M/1 finden sich vorn Protoconid, Metaconid, linguales und labiales Anteroconid als gut differenzierte Höcker. Unterschiede zu *M. hortulanus* am Jochbogen sind nicht überprüfbar, doch spricht die bedeutende Zahngröße (M1/ = 1.84 × 1.00 mm) für *M. abbotti.*

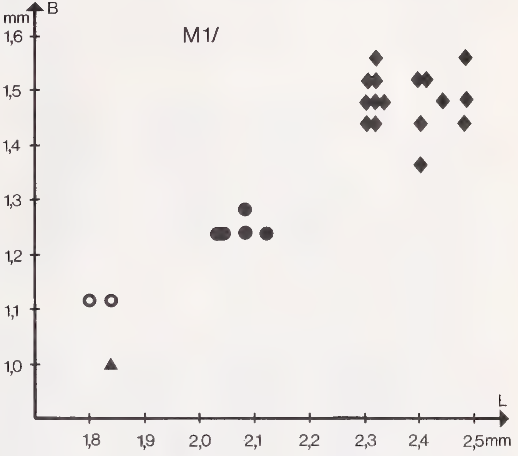


Abb. 1. Größte Längen (L) und Breiten (B) von M1/ der in Karain B vertretenen Muriden-Arten; alle Jungpleistozän. ◆ *Apodemus mystacinus,* ● *Apodemus flavicollis,* ○ *Apodemus sylvaticus,* ▲ *Mus abbotti*

Gattung Apodemus

Apodemus mystacinus (Danford und Alston, 1877): Die M1/ zeigen ausnahmslos das für pleistozäne und rezente anatolische Populationen kennzeichnende *mystacinus*-Muster (Storch 1975, 1977; Kuss und Storch 1978). T12 ist mit t9 und t8 verbunden, und die Verbindung t9–t12 ist zumindest so gut entwikkelt wie die von t8–t9. Bei dem balkanischen *epimelas*-Muster hingegen steht t12 schlußcingulum-artig nur mit t8 in Verbindung. In der Konfiguration des t12 unterscheiden sich die beiden anderen *Apodemus*-Arten aus Karain B von *A. mystacinus: A. flavicollis* besitzt einen schlußcingulum-artigen t12, der an dem kleineren und zierlicheren M1/ von *A. sylvaticus* höchstens schwach angedeutet ist. *A. mystacinus* von Karain hat im Mittel etwas größere M1/ als heutige westanatolische Tiere, stimmt aber gut mit jung-mittelpleistozänem Material von Chios überein (Storch 1975).

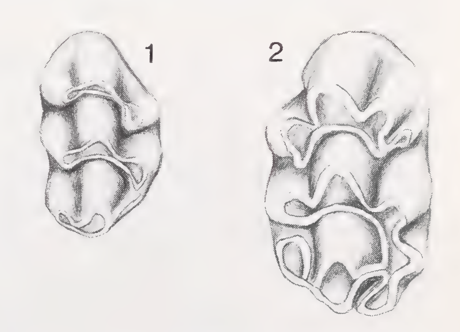


Abb. 2. M1/ von Karain B in Occlusalansicht. 1 = *Mus abbotti,* 2 = *Apodemus mystacinus*

Gattung Microtus

Microtus (Chionomys) gud Satunin, 1909: Die M3/ aus dem Jungpleistozän von Karain B

Tabelle 2. **Zahnmaße der drei *Microtus*-Arten von Karain B, SW-Anatolien**

	M/1			M3/		
	n	x̄	Var	n	x̄	Var
Microtus gud	25	2.8	2.4–3.1	11	2.2	2.0–2.3
Microtus guentheri	35	3.3	3.0–3.6	12	2.3	2.1–2.6
Microtus arvalis	11	2.7	2.4–3.0	7	1.9	1.8–2.0

stimmen mit denen rezenter Tiere von dem einzig bekannten Fundpunkt im Taurus (bei Ulukişla im östlichen Mitteltaurus; Spitzenberger 1971) überein. Beide besitzen ein normalis-Muster, d.h. 3 Labial- und 4 Lingualantiklinalen. Sie unterscheiden sich hierin von Populationen des heutigen ostpontisch-kaukasischen Areals der Art, die ausnahmslos komplexer gebaute M3/ besitzen (Spitzenberger 1971; Steiner 1972). Die M/1 stimmen dagegen überein. Der kennzeichnende Vorderlobus besteht aus einem konfluenten Dentinfeld und besitzt 2 Lingualantiklinalen und eine mehr oder weniger ausgeprägte labiale Kante. Es kommt nicht zur Abschnürung der Vorderkappe wie bei *M. nivalis* oder zu einer völlig gerundeten Labialkontur des Vorderlobus wie bei *M. oeconomus.* Die rezente und die jungpleistozäne Population aus dem Taurus sind durch ihre M3/ gut charakterisiert, und sie sollten gegen die ostpontisch-kaukasischen Populationen subspezifisch abgegrenzt werden.

Die Zuordnung isolierter M3/ zu den vertretenen *Microtus*-Arten erscheint mir relativ unproblematisch. Die M3/ von *M. guentheri* sind am kompliziertesten und besitzen charakteristische distale Enden (vgl. Besenecker et al. 1972; Storch 1975). Die M3/ von *M. arvalis* sind einfach und weisen verrundete Distalenden auf (vgl. Storch 1975). Darüber hinaus sind die M3/ von *M. arvalis* kleiner und zierlicher, was besonders in Seitenansicht auffällt. Es gibt keine zierlichen und gleichzeitig kompliziert gebauten M3/ als Hinweis auf *M. socialis.*

Die M/1 von *M. guentheri* und *M. arvalis* unterscheiden sich außer in der Größe in der von Storch (1975) dargelegten Weise. So besitzt *M. guentheri* ausgedehntere, aufgeblähte Vorderkappen mit häufiger Kantenbildung, während *M. arvalis* relativ zierliche Vorderkappen aufweist. (Es scheint unklar zu sein, ob in Kleinasien heute *M. arvalis* oder *M. epiroticus* vorkommt. Die vorliegenden Zähne können nicht zu einer Entscheidung beitragen, und *arvalis* ist als konventioneller Gebrauch des Artnamens zu verstehen.)

M. guentheri aus dem Jungpleistozän von Karain B weist deutlich größere M/1 auf als heutige westanatolische Tiere und als eine jung-mittelpleistozäne Population von Chios. Gute Übereinstimmung besteht jedoch zu altholozänem Material von Chios, das sich auch in seinen Skelettmaßen als sehr großwüchsig erweist (Besenecker et al. 1972; Storch 1975).

Gattung Arvicola

Arvicola sp.: Das Schmelzband der M/1 ist auf der konkaven und der konvexen Prismenseite gleichdick („*cantiana*"-Muster). Dieses Stadium vermittelt zwischen der Konfiguration bei *Mimomys savini* und den stratigraphisch frühesten *Arvicola*-Arten (konvexes Schmelzband verstärkt) einerseits und dem Muster heutiger mitteleuropäischer *A. terrestris* (konkaves Schmelzband verstärkt) andererseits. Biostratigraphische Einstufungen anhand solcher Entwicklungen sind unter Umständen für einen Ausschnitt, nicht jedoch über das Gesamtareal der Gattung durchführbar. Die Schmelzbänder rezenter *A. terrestris* zeigen eine Kline vom typischen *terrestris*-Muster in W- und Mitteleuropa bis zur typischen „*cantiana*"-Form in Vorderasien (Röttger 1986). Das jungpleistozäne Material stimmt hinsichtlich der Schmelzbanddifferenzierung mit heutigen SW-asiatischen Populationen überein, und es ist darin fortschrittlicher als *A. praeceptor* aus dem jüngeren Mittelpleisto-

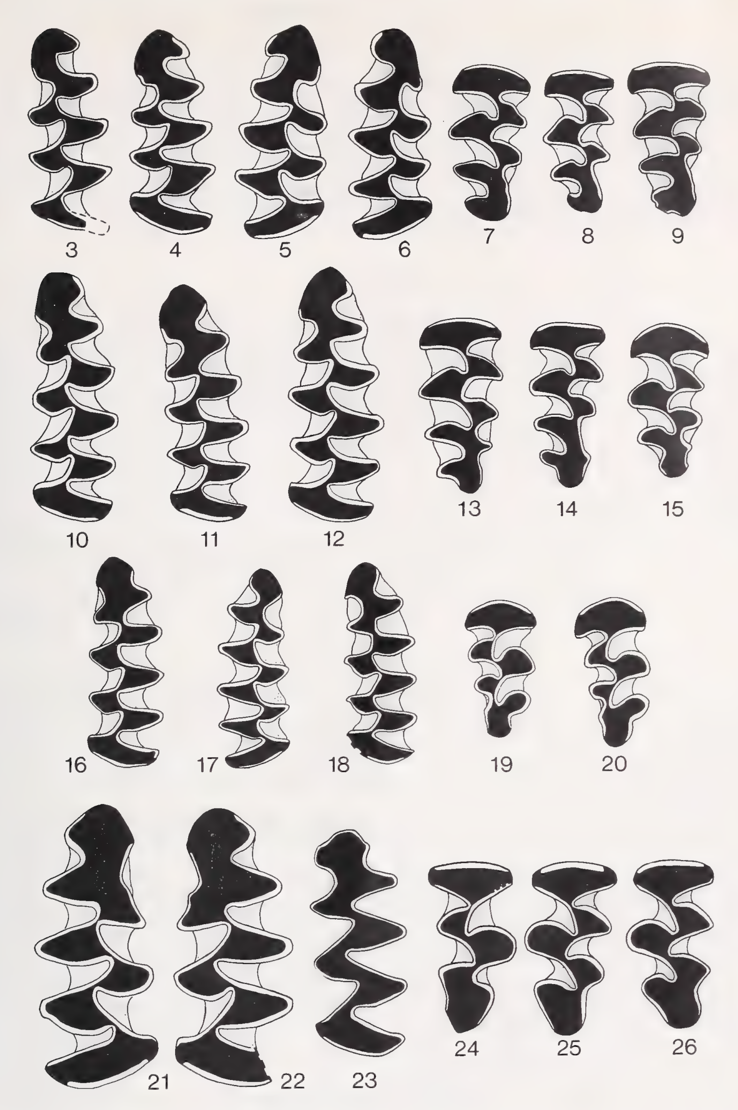


Abb. 3. Arvicolidenzähne von Karain B in Occlusalansicht. *Microtus gud:* 3–6 = M/1, 7–9 = M3/; *Microtus guentheri:* 10–12 = M/1, 13–15 = M3/; *Microtus arvalis:* 16–18 = M/1, 19–20 = M3/; *Arvicola* sp.: 21–23 = M/1, 24–26 = M3/

zän von Chios (Storch 1975). Der Artname wird zunächst offengelassen, bis besser erhaltenes Material die Überprüfung auch anderer Merkmale erlaubt.

Zahnmaße von *Arvicola* sp. aus Karain: M/1 = 3.1–3.8, M3/ = 2.3–2.4 mm.

Danksagungen

Herr Dr. Gerd Albrecht als örtlicher Grabungsleiter hat mir dankenswerterweise die Kleinsäugerfauna überlassen. Die Zeichnungen fertigte Frau A. Helfricht, Senckenberg-Museum, an.

Zusammenfassung

Ausgehend von günstigeren Umweltverhältnissen im Mittelpaläolithikum nahmen im Älteren Jungpaläolithikum Aridität und Offenland zu. Bei fortbestehender Dominanz von Steppenverhältnissen zeichnen sich im „Epipaläolithikum" kürzere klima-ökologische Oszillationen ab. *Microtus gud* wurde offenbar gebietsweise durch den weniger hygrophilen *M. nivalis* als spätem Immigranten von Westen her ersetzt. *Mus abbotti* erscheint gegen Ende der pleistozänen, *Meriones tristrami* erst mit holozänen Schichtenfolgen. Einige Arten verschwinden im Jungpleistozän für immer aus dem Gebiet; trotzdem ist eine bedeutende ökologische und faunistische Stabilität zu erkennen.

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Z. Säugetierkunde 53 (1988) 83–91

ISSN 0044-3468

Vocalizations of captive Water mongooses, *Atilax paludinosus*

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Receipt of Ms. 11. 2. 1987

Abstract

The vocalisations of water mongooses were recorded and analysed sonagraphically. Three main types of sounds were recognised, namely "bray types", "grizzle types" and "humph types". "Bray types" were produced during mating and also in some agonistic encounters. "Grizzle types" were produced by both old and young animals and indicated either distress or a warning. "Humph types" were the only sounds that were characterised by some frequency modulation and were interpreted as either attention or appeasement calls. Compound calls were also recorded and consisted of two or more of the above types produced in rapid succession. It is suggested that the few sounds made by *Atilax* represent the basic pattern from which the more complex vocal patterns of sociable herpestines have developed. This suggestion does not, however, assume that the calls of *Atilax* are primitive, as they are well adapted to the mongooses way of life.

Introduction

The variety of vocalisations produced by water mongooses is limited, unlike those of the Indian mongoose *Herpestes auropunctatus* (Mulligan and Nellis 1975), the dwarf mongoose, *Helogale undulata rufula* (Maier et al. 1983) the banded mongoose, *Mungos mungo* (Garratt 1978) and the suricate *Suricata suricatta* (Ewer 1973). Water mongooses are solitary and nocturnal or crepuscular herpestines. Although relatively silent on their own, the variety of calls produced during social interactions indicates their ability to communicate adequately when necessary. However, the limited vocal repertoire of *Atilax,* when compared with the extensive and complex repertoire of sociable herpestines (Ewer 1973; Garratt 1978), indicates that sociable mammals develop a wider vocabulary in response to the demands of group living. In addition to vocalizations, water mongooses communicate behaviourally through facial expression and body posture as well as through chemical means. Both behavioural and chemical communication will be presented elsewhere.

Material and methods

The data presented here were obtained from eight captive water mongooses which were housed either singly or in pairs in outdoor enclosures measuring 1,5 × 3 × 1,2 m. Details regarding their maintenance are given in Baker (1987) and Baker and Meester (1986). Recordings were made on an Uher 4000 Report-L tape recorder at a speed of 9,5 cm using either an Uher M517 microphone or a D.K.G. model D58E directional microphone. Acoustic analysis was performed using a Kay Sonagraph 7029A. For most of the recordings a frequency range of 80 to 8000 Hz was selected, although 40 to 4000 Hz was used for sounds of low frequency. In all cases the narrow filter bandwidth of 45 Hz was selected.

Although attempts were made to eliminate background noise during recording sessions, many sonagrams show low frequency noise.

The parameters that were described for each sonagram are defined as follows (Eisenberg et al. 1973; Rossing 1982):

1. Fundamental frequency: The component of a sound of the lowest frequency;
2. Harmonics: The components of a sound whose frequencies are multiples of the frequency of the fundamental frequency;
3. Duration: Time of each call or its components (syllables);

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4. Syllable: Basic call element that manifests itself as an uninterrupted tracing on the horizontal axis of the sonagram;
5. Phrase: Group of syllables separated from other syllables by a time interval greater than any time interval separating the syllables in a phrase;
6. Tonal syllable: Harmonic syllable;
7. Noisy syllable: Sound not organised into discrete energy bands;
8. Mixed syllable: Appears on a sonagram as a superimposition of noise upon a harmonic series;
9. Long syllable: More than 0,6 seconds in duration;
10. Short syllable: Exceeds 0,05 seconds and less than 0,6 seconds in duration;
11. Formant: A range of frequency to which a system responds preferentially or which is emphasised in its output.

The context in which the sounds were made was recorded and briefly described.

Results

One hundred and forty-three sounds were sonagraphed and classified into three main types (Fig. 1). Each type was further divided into different forms showing basic similarities. Type one, called "bray types", consists of long or short mixed syllables which

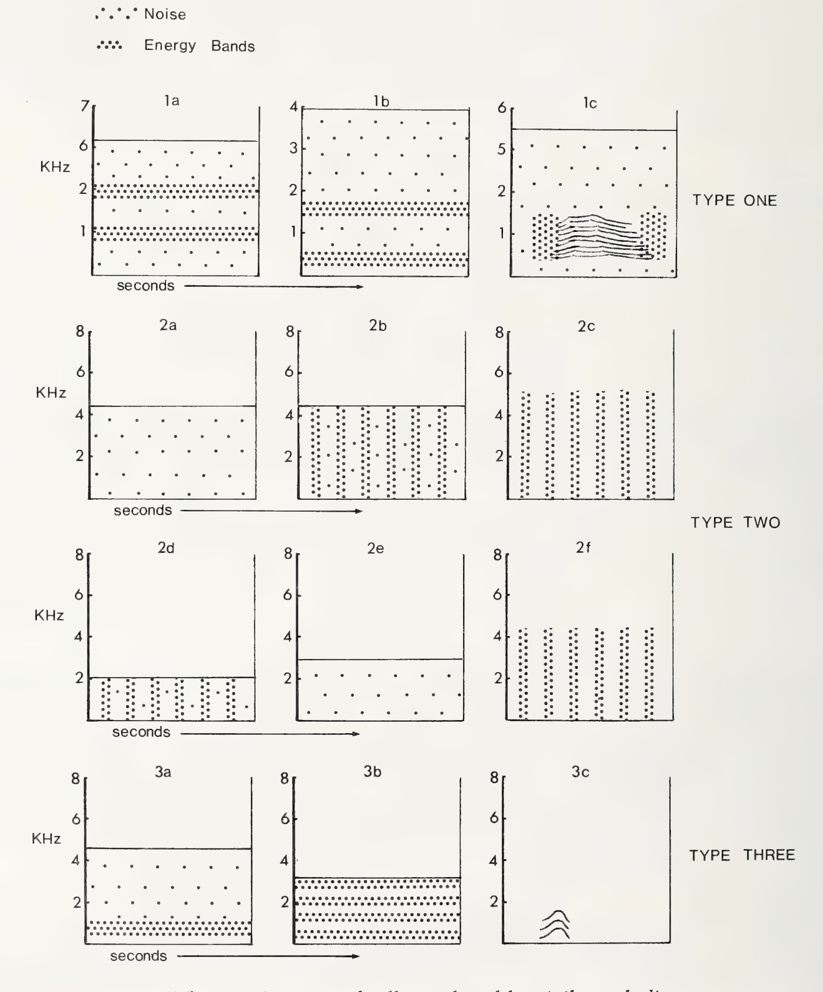


Fig. 1. Three main types of calls produced by *Atilax paludinosus*

Table 1. **Variation in Type 1 calls**

	Type 1a		Type 1b		Type 1c		ANOVA		
	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	F	P	S
Duration	0.65	0.26	0.99	0.79	0.86	0.86	0.79	0.48	NS
Fundamental frequency	1	–	0.58	0.26	0.5	–	9.63	0.007	S
Harmonic number	1	–	1	–	14	–	–	–	–
Maximum frequency	6.29	1.79	3.93	0.51	5.5	–	3.65	7.25	NS

exhibit pronounced bands of energy. Type two, called "grizzle types", are characterised by the presence of pulses. The calls vary in amplitude, and may be long or short and noisy or mixed. Type three, called "humph types" are short, with tonal or mixed syllables. Some frequency modulation is usually apparent.

Type one: The three different forms of this call (n = 12) are produced mainly in the context of mating (75 %) and also in some agonistic encounters (25 %). During a mating sequence it is always the female that produces the sound during the initial chase and avoidance phase when she attempts to escape the male. In aggressive encounters it is always the subordinate that calls. The posture of this animal is characteristically submissive with the shoulders at a lower height than the haunches, and often the head is tilted upwards or backwards, pointing towards the dominant animal. The mouth is usually wide open.

Forms 1a and 1b (Fig. 2) are very similar (Table 1) but are significantly different with

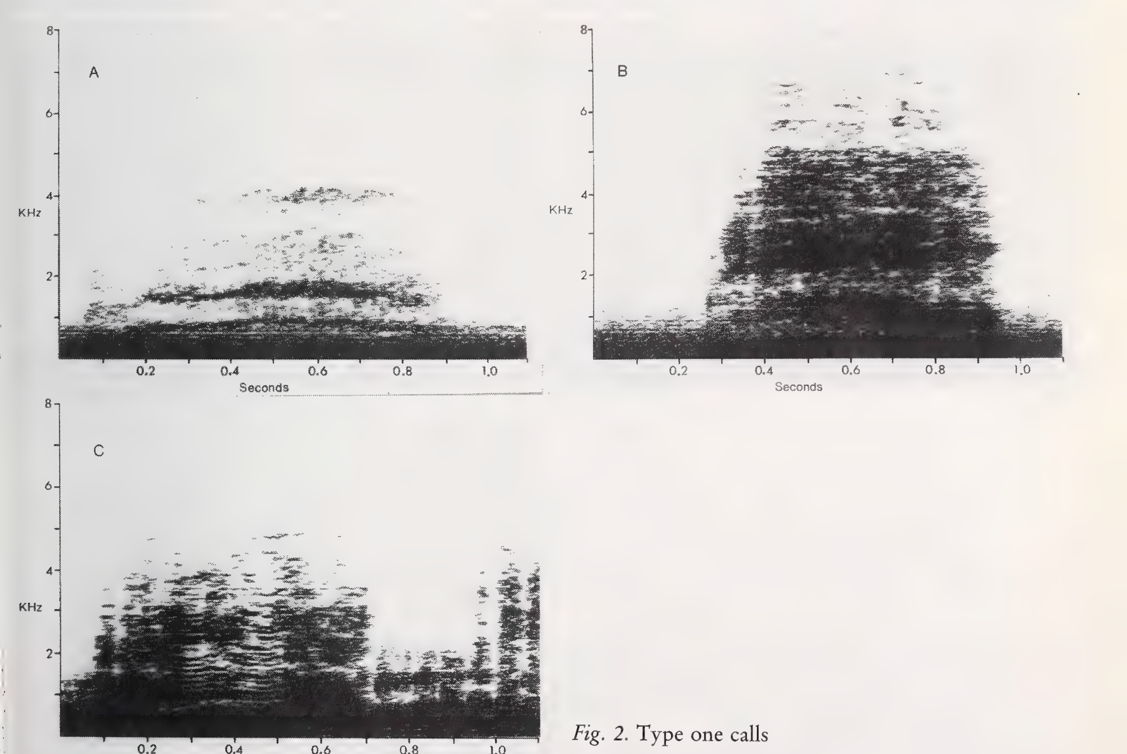


Fig. 2. Type one calls

Table 2. **Variations in Type 2 calls**

	Type 2a		Type 2b		Type 2c		Type 2d		Type 2e		Type 2f			ANOVA	
	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	F	P	Signif.
Duration	0.98	0.46	0.85	0.6	0.31	0.31	1.37	1.47	1.14	0.87	0.97	0.73	2.65	0.02	S
Maximum freq.	4.54	1.04	4.5	0.97	5.12	1.60	2.00	0.93	3.08	0.64	4.58	2.20	0.69	0.62	NS
Formant	1.61	0.56	1.79	0.67	1.81	0.37	0.66	0.14	0.89	0.3	1	–	9.62	0.000001	S
No. of pulses	–	–	9.03	7.6	4.25	0.5	24.3	20.03	–	–	7.66	3.88	6.52	0.0008	S

respect to their fundamental frequencies (t = 3,92; p = 0,004; df = 8) and maximum frequency (t = 2,51; p = 0,036; df = 8). Form 1c (Fig. 2) is clearly different from 1a and 1b due to the presence of more than one harmonic. However, there are marked similarities in duration, maximum frequency and fundamental frequency (Table 1). Form 1c was produced exclusively prior to mating.

All three of these forms may be repeated within 0,6 seconds, usually depending on the intensity of interaction between two mongooses.

Type two: Table 2 shows the main parameters of these forms (n = 94). There are clearly two groups, one of a higher frequency (2a, 2b, 2c) than the other (2d, 2e, 2f) (Fig. 3). The sounds are made equally by both adults and juveniles, although 2c is exclusively an adult sound.

In most instances (52,1 %) these calls indicated distress, resulting from frustration of goal-directed behaviour. In social encounters they are most commonly produced by a submissive animal during agonistic displays (40,4 % of the time). Grizzles are the sounds most commonly found in captive handraised animals, probably resulting from their restriction. Wild, captive mongooses produce these "grizzle" sounds (2a, 2b, 2f and 2e) (Fig. 3) only in the context of agonistic encounters or in parent-young interactions. In agonistic encounters they often precede a confrontation and are produced by the submissive animal. In parent-young interactions the sound may be made by the mother when she is avoiding her offspring, in which case it serves as a warning, or when she is engaged in play-fighting. During these sequences it is the young that call as they are clearly subordinate to the mother. The young "grizzle" when left alone by the mother indicating that they are disgruntled; when playing roughly with each other or their mother as a form of protest; and also when unwilling to be groomed by the parent. In the last two situations the call signals a need to be released.

Form 2e (Fig. 3) is primarily produced by very young animals (96,4 % of the time, n = 28) and never exhibits pulses. It is a low frequency, noisy sound which may have a formant at 0,89 Hz on average (n = 28, SD = 0,3). It is mostly used when the parent leaves the nest for foraging or when the young have managed to emerge from the nest and are clearly disorientated.

Form 2d (Fig. 3) is a growl which is distinct from the others in always being of low frequency, and varying widely in duration (Table 2). The pulse frequency is remarkably constant at 0,025 seconds. Of the 14 incidences of growling 14,2 % were made during mating sequences, 50 % were feeding growls and the remainder (35,8 %) were threats made by adults towards the observer.

Form 2c (Fig. 3) is a cackle produced by adults. It is a

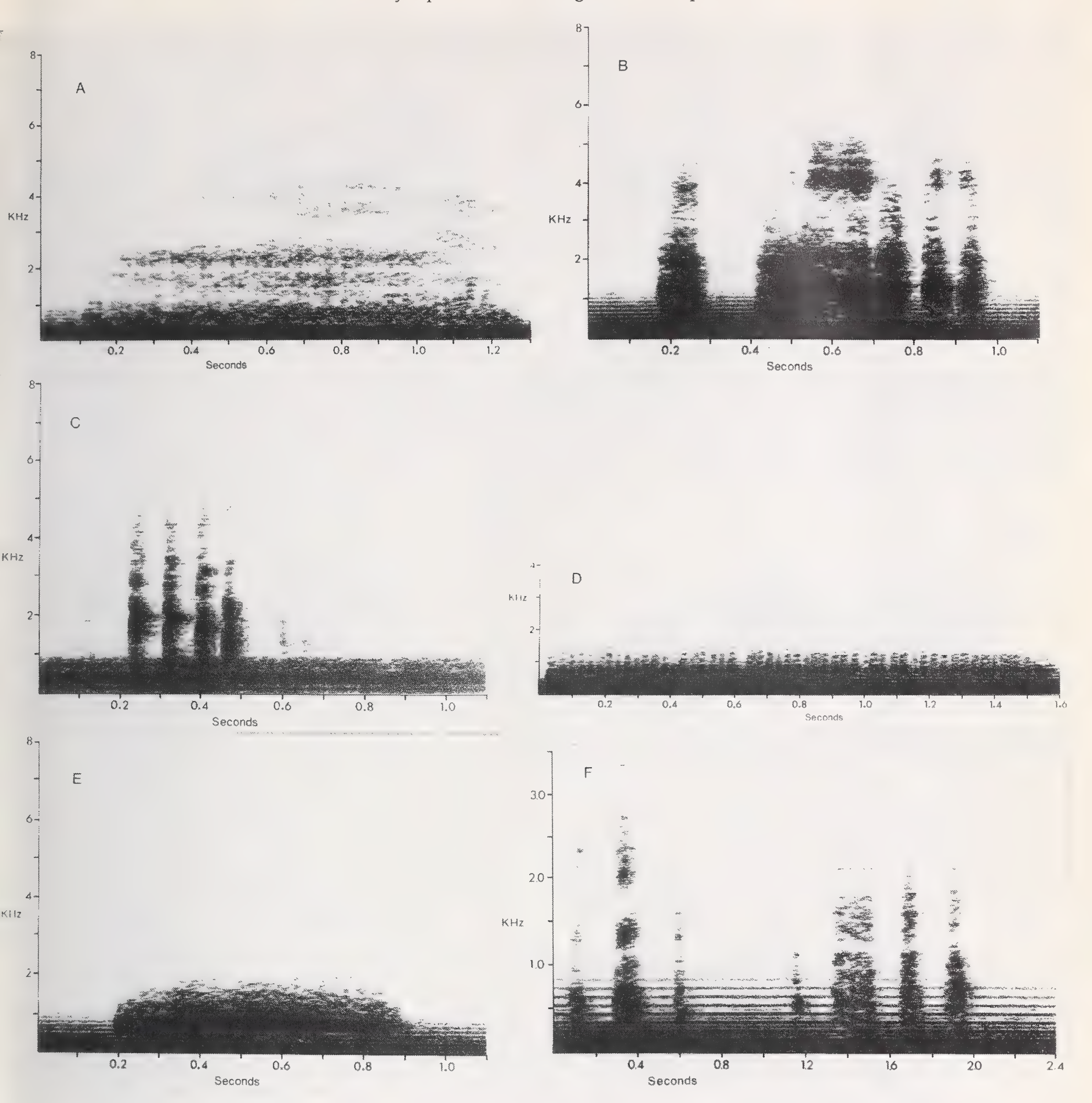


Fig. 3. Type two calls

loud explosive, clear and concise sound. The growl and the cackle are produced as a threat or when surprised.

The pulse interval in type two calls varies from 0,025 seconds to 0,28 seconds, $\bar{x}$ = 0,07 seconds, SD = 0,04.

Type three: The main parameters of type three calls n = 37 are presented in Table 3.

Both young and older animals produce these calls, although 3c is exclusively produced by very young mongooses when calling for attention. Forms 3a and 3b (Fig. 4) were also made to attract the attention of the parents. In older animals 3a and 3b were often produced in anticipation of food. During mating sequences the male was heard calling

Table 3. **Variations in Type 3 calls**

	Type 3a		Type 3b		Type 3c		ANOVA		
	x̄	SD	x̄	SD	x̄	SD	F	P	Signif.
Duration	0.28	0.04	0.32	0.13	0.28	0.06	0.99	0.37	NS
Maximum frequency	4.58	1.49	3.26	1.03	1.75	0.28	11.56	0.0001	S
Fundamental frequency	–	–	0.56	0.11	0.51	0.04	0.84	0.37	NS
Harmonic No.	–	–	5.87	2.58	2	0.03	12.64	0.003	S
Max. freq. modulation	–	–	–	–	0.35	6.64	–	–	–

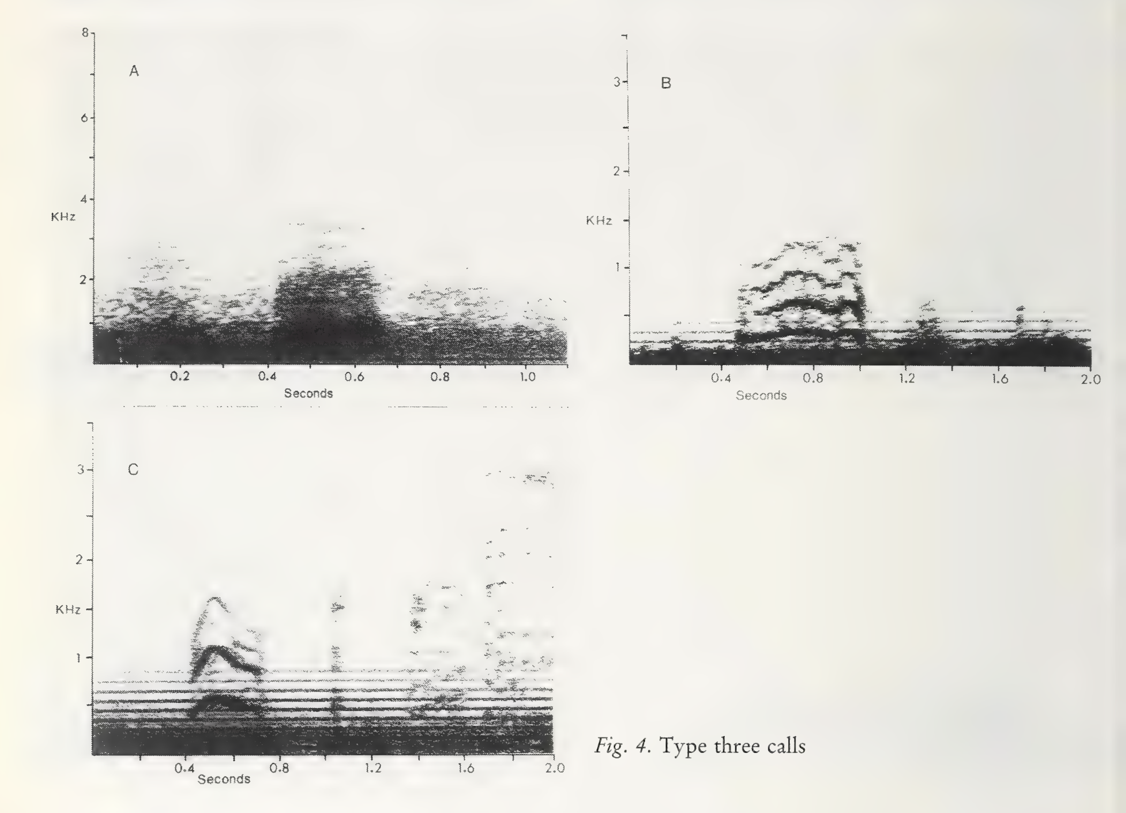


Fig. 4. Type three calls

when confronted with an unwilling female. Because this sound was made only in response to a female threatening a persistent mate (in the context of mating) during the initial phases of the mating sequence, it indicates an appeasement function.

Form 3c exhibits a marked frequency modulation (Fig. 4; Table 3), and is the only water mongoose call to do so.

Occasionally different sounds were grouped together to form a compound call. Most commonly "grizzle" sounds were repeated to form a phrase, although some sounds consisted of a series of the above types following one another sequentially, or superimposed one upon the other (Fig. 5). Most commonly there was a combination of types two and three, beginning with a "grizzle" and ending with a "humph". Type two ("grizzle") might also be followed by a type one sound ("bray").

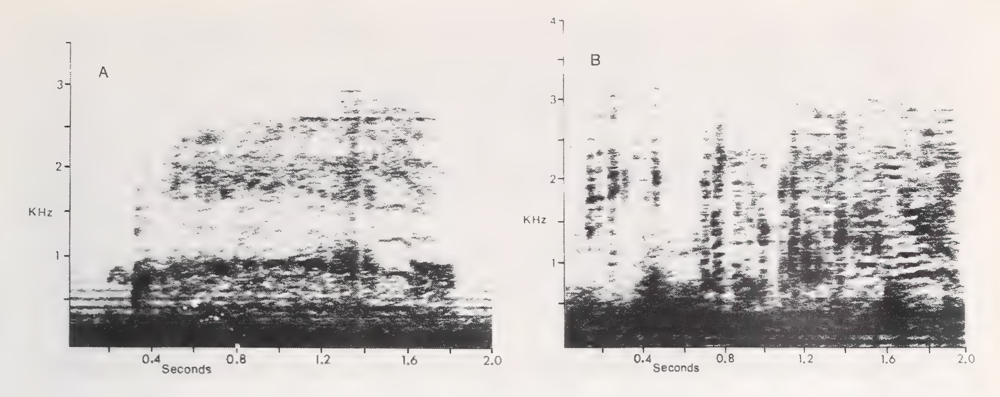


Fig. 5. Compound calls produced by *Atilax.* A: Grizzle followed by humph; B: Grizzle followed by bray

Discussion

Although the variety of vocal sounds made by captive *Atilax* is poor, their inherent variability is extensive, especially when duration and maximum frequency are considered.

The only other major variant is the number of pulses that occurs in Type 2 calls. This is clearly related to duration, as the longer the calls the greater the number of pulses. The variation in pulse intervals shows no clear pattern, and is neither sex- nor age-related, as both young and old animals exhibit both extremes of the range.

Eisenberg et al. (1973) discuss variability within the categories of sounds produced by marsupials, and note that a number of transitional forms of the defined type may exist, such that the distinctness of two types becomes confused. Further, the sounds that are used as the categorical type are usually at the extremes of a graded series of sounds, and thus are quite distinct. In *Atilax* there are some sounds that may structurally appear to fit into one category or another, such as types 1a, 2a and 3a sounds. It is often only the auditory perception of the sound in conjunction with its visual context that provides the key to the category in which it belongs.

The variation in *Atilax* calls may have one or more of several determinants, most notably individual variation or age-related differences. In addition, a solitary mongoose with its limited vocal repertoire demands less specificity with respect to the sounds that it makes, as there is little chance of confusion when so few calls make up the entire vocabulary. In a social animal with a wider range of different calls it becomes important to ensure correct understanding of specific signals, as these are crucial in maintaining group understanding. Therefore it would be expected that greater attention would be paid to pronouncing the sounds concisely.

The tendency in colonial birds (Wiley 1976) is towards reduction in the variety and detail of calls as these become confused in the noisy environment of a breeding colony. This may be an important factor influencing the vocalisations of mammals, and would be most clearly illustrated amongst some of the sociable herpestines. However, the available information on vocal repertoires of sociable mongooses indicates a deviation from this pattern, which may also be representative of other mammalian groups.

When compared with vocalisations of *Mungos mungo* (Garratt 1978) and *Herpestes auropunctatus* (Mulligan and Nellis 1975) it becomes clear that the sounds made by *Atilax* are a basic type that is found within the repertoire of these other two species, and which has in some instances been slightly modified (e.g. the weeonk call of *Herpestes*

auropunctatus resembles the "humph" call of *Atilax*) or elaborated upon (e.g. the squeal and "we" calls of *Mungos mungo* share similarities with the "humph" of *Atilax*).

By virtue of their solitary nature water mongooses have no need of a "moving out call" or a contact call (Maier et al. 1983) as these are particularly related to aspects of group life. The sounds produced by the water mongoose may represent those that are essential for maintaining compatibility during their comparatively brief encounters and perhaps it is not surprising that the sounds made most commonly by adults were related to either agonistic behaviour or distress. The captive conditions are likely to have induced a greater usage of these two kinds of sounds, and in the natural environment their incidence may be greatly reduced. It was only the "humph" call that elicited an amicable response in captivity, although some of the type 2 calls (Type 2e) made by juveniles were used to elicit a positive response from either siblings or parent.

In general the sounds made by *Atilax* are of low frequency and are remarkably simple, and it is suggested that they represent an example of the basic pattern from which the more complex vocal repertoires of other herpestines have developed. Busnel (1963) supports this suggestion, and comments that the number of signals made by animals vary, but that in general their number increases 'the higher one goes in the Animal Kingdom'. Nevertheless the fact that the sounds made by *Atilax* may represent a basic pattern does not necessarily mean that they are primitive, as water mongooses are clearly well adapted to their environment. Indeed, *Atilax* has developed specialised, but simple techniques for optimising survival in its particular niche.

Acknowledgements

Thanks are due to the following people: Professor J. Meester for supervising the project and reading the manuscript; Ms A. Nolte and Dr P. Wakerley for allowing access to the sonagraphic equipment in the Department of Physics; Professor O. A. E. Rasa and Mr D. Basckin for reading and commenting on the manuscript; Professor G. Maclean for translating the summary; Mr D. M. Dlamini for preparing photographs of the sonagrams. Financial assistance from the South African Council for Scientific and Industrial Research and the University of Natal, Durban, is gratefully acknowledged.

Zusammenfassung

Vokalisationen des Sumpfichneumon, Atilax paludinosus, in Gefangenschaft

Die Lautäußerungen von Sumpfichneumons in Gefangenschaft wurden aufgenommen und sonagraphisch analysiert. Drei Haupttypen von Lauten konnten unterschieden werden: Schreien, Murren und „Hm"-Laute. Schreilaute wurden hauptsächlich während der Paarung geäußert, aber auch in einigen agonistischen Verhaltensweisen. Laute des Typs Murren wurden von alten und auch jungen Tieren wiedergegeben, entweder in einer Notlage oder als Warnung. „Hm"-Laute, die einzigen Laute, die durch Frequenz-Modulation charakterisiert sind, dürfen als Achtungs- oder Beruhigungslaute bezeichnet werden. Zusammengesetzte Rufe wurden ebenfalls analysiert. Sie bestanden aus zwei oder mehr der oberen Typen, die schnell nacheinander geäußert wurden. Es wird angenommen, daß die wenigen Lauttypen des solitären *Atilax* ein Basis-Muster darstellen, aus dem sich die komplizierteren Muster sozialer Herpestinae entwickelt haben könnten. Diese Annahme sollte jedoch nicht zu der Aussage verleiten, daß die *Atilax*-Rufe primitiv seien, denn sie sind der Lebensweise dieser Mangustenart gut angepaßt.

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Z. Säugetierkunde 53 (1988) 92–101

ISSN 0044-3468

Secondary sex ratio in the Przewalski horse *Equus przewalskii* (Mammalia: Equidae)

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Receipt of Ms. 16. 3. 1987

Abstract

Sex ratio distribution in sibships and the relation between the secondary sex ratio and maternal age, paternal age, parity, birth sequence, season and year were studied in the Przewalski horse *Equus przewalskii.* No variations of the secondary sex ratio in relation to the studied factors were detected; sex ratio distribution was found to be simply binomial, i.e. random. The overall secondary sex ratio was found to be not significantly different from unity both in Przewalski horses and in other perissodactyls.

These data neither support, nor directly contradict, the theory that females are capable of adjusting the sex ratio of their offspring.

Introduction

Variations in the secondary sex ratio represent an important component of the Trivers and Willard's (1973) hypothesis of the adaptive value of the female's ability to adjust facultatively the sex of its offspring (see also Burley 1982), which in turn forms a part of the parental investment theory (Trivers 1972; Maynard Smith 1977, 1980; Clutton-Brock and Albon 1982), and are thus of considerable theoretical interest. Despite this, data relevant to the problem are still rather scarce, even in mammals (Clutton-Brock and Albon 1982; Bol'šakov and Kubancev 1984; Clutton-Brock 1986a) and birds (Clutton-Brock 1986b). In the present paper I will contribute to the problem under discussion by analyzing the secondary sex ratio in the Przewalski horse *Equus przewalskii* Poljakov, 1881.

Captive Przewalski horses seem to be suitable for this purpose for the following reasons: They are strictly monotocous (Mohr and Volf 1984), so that variations in the litter size are ruled out (cf. Smith and Fretwell 1974; Myers 1978; Gosling 1986b); they are free of nutritional stresses which were found to be important in this respect (cf. Rivers and Crawford 1974; McClure 1981; Van der Merwe and Skinner 1982; Silk 1983; Verme 1983, 1985; McGinley 1984); and they do not suffer from predation (cf. Berger 1983). It could be thus expected that the effect of the remaining factors on the secondary sex ratio will be more pronounced and easier to detect.

Material and methods

All of the demographic data used in the present paper were extracted from the published Pedigree Books of the Przewalski Horse (Volf 1980, 1981, 1982, 1983, 1984). They are, hence, considering captive animals. Overall, data on 1115 newborn foals were obtained, produced by 262 mares and 113 staillons. In testing the results, standard statistical procedures were employed (Sokal and Rohlf 1969; Sachs 1974).

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Results

Overall secondary sex ratio

Of the 1115 newborn Przewalski foals of known sex registered in the Pedigree Books 529 (= 47.44 %) were males and 586 (= 52.56 %) females. The slight preponderance of females is statistically not significant (see Tab. 1).

To see whether this is a specific feature of Przewalski horses, or whether the 1:1 secondary sex ratio is typical for horses and other perissodactyls, I compiled the relevant data from the "Mammals bred in captivity and multiple generation births" section of the International Zoo Yearbook, vols. 1–23 (Tab. 1). The data show convincingly that in not one of the listed species the secondary sex ratio significantly deviates from unity, although rhinos posses some tendency to bear more males than females ($p = 0.065$).

Effect of maternal age

The ability to parental investment varies with the female's age (CASWELL 1982, 1984), so that it could be expected that the secondary sex ratio will vary with the female's age as well. Indeed, such a variation has been reported for European bisons *Bison bonasus* (ZABLOCKIJ 1957), red deer *Cervus elaphus* (LOWE 1969), white-tailed deer *Odocoileus virginianus* (VERME 1983, 1985), barbary macaques *Macaca sylvanus* (PAUL and THOMMEN 1984),

Table 1. **Overall secondary sex ratio in wild (w), feral (f) and captive (c) Perissodactyla**

Taxon		N	N♂ (% ♂)	N♀ (% ♀)	N♂/N♀	G_{adj}	References
Equus przewalskii	c	1115	529 (47.44)	586 (52.56)	0.903	1.358	this study
Equus caballus	f	476	248 (52.10)	228 (47.90)	1.088	0.341	WELSH 1975; FEIST and McCULLOUGH 1975, 1976; BERGER 1977, 1983; KEIPER 1979; NELSON 1980
Equus hemionus	c	772	400 (51.82)	372 (48.19)	1.075	0.438	this study
Equus africanus	c	72	36 (50.00)	36 (50.00)	1.000	0.028	this study
Equus asinus	f	23	7 (30.43)	16 (69.57)	0.438	1.113	McCORT 1979
Equus zebra	w	46	19 (41.30)	27 (58.70)	0.704	0.395	PENZHORN 1975
Equus zebra	c	276	141 (51.09)	135 (48.91)	1.044	0.029	this study
Equus quagga	w	216	114 (52.78)	102 (47.22)	1.118	0.232	SMUTS 1976
Equus quagga	c	2793	1340 (47.98)	1453 (52.02)	0.992	2.207	this study
Equus grevyi	c	622	323 (51.93)	299 (48.07)	1.080	0.389	this study
Equidae		6411	3157 (49.24)	3254 (50.76)	0.970	0.704	
Tapirus indicus	c	120	61 (50.83)	59 (49.17)	1.034	0.001	this study
Tapirus terrestris	c	446	225 (50.45)	221 (49.55)	1.018	0.004	this study
Tapirus bairdi	c	19	12 (63.16)	7 (36.84)	1.714	0.241	this study
Tapirus pinchaque	c	6	3 (50.00)	3 (50.00)	1.000	–	this study
Tapiridae		591	301 (50.93)	290 (49.07)	1.038	0.069	
Rhinoceros unicornis	c	37	24 (64.86)	13 (35.14)	1.846	1.122	this study
Ceratotherium simum	c	148	87 (58.78)	61 (41.22)	1.426	1.963	this study
Diceros bicornis	c	116	63 (54.31)	53 (45.69)	1.189	0.276	this study
Rhinocerotidae		301	174 (57.81)	127 (42.19)	1.370	3.388	

N = number of newborn animals sexed. G_{adj} = WOOLF's (1957) log likelihood ratio test, adjusted after YATES, two-tailed. No deviations are significantly different from unity ($p > 0.05$).

captive coypus *Myocastor coypus* (Gosling 1986a), captive foxes *Alopex lagopus* (Žegalov 1950), various species of domestic mammals (see Bol'šakov and Kubancev 1984 for review) and in man (e.g., Mlíkovský 1987). On the other hand, no such variation was revealed in Przewalski horses (this study, Tab. 2) and in rhesus monkeys *Macaca mulatta* (Rawlins and Kessler 1986).

Effect of paternal age

In equids, males do not care for foals (Groves 1974), so that no variation in the secondary sex ratio with the paternal age is to be expected on the basis of the parental investment theory. However, other mechanisms, such as physiological, may cause this relationship. The results show that the secondary sex ratio does not vary with the paternal age in Przewalski horses (Tab. 3), which agree in this respect with red deer (Clutton-Brock et al. 1981) and domestic mice *Mus musculus* (Suntzeff et al. 1962). However, such a variation was described in pine martens *Martes martes* (Grakov 1969), various species of domestic mammals (Kamaljan 1962; Bol'šakov and Kubancev 1984) and in man (e.g., Pollard 1969; Mlíkovský 1987).

Effect of parity

The effect of parity on the secondary sex ratio has been little studied thus far and seems to have no direct theoretical interpretation. Przewalski horses showed no variation of the secondary sex ratio with parity (Tab. 4). The same result has been reported also for rhesus monkeys (Rawlins and Kessler 1986) and domestic pigs *Sus scrofa* (Kennedy and Moxley 1978; Gray and Katanbaf 1985).

Table 2. **Relation between the secondary sex ratio and maternal age (at delivery) in *Equus przewalskii*, based on the offspring of 262 mares**

Age (Year)	N	N♂ (% ♂)	N♀ (% ♀)	N♂/N♀	χ^2_{adj}
2	1	1	–	–	–
3	60	28 (46.67)	32 (53.33)	0.875	0.001
4	104	54 (51.92)	50 (48.08)	1.080	0.668
5	117	60 (51.28)	57 (48.72)	1.053	0.547
6	108	49 (45.37)	59 (54.63)	0.831	0.112
7	91	44 (48.35)	47 (51.65)	0.936	0.005
8	91	37 (41.66)	54 (59.34)	0.685	1.417
9	78	30 (38.46)	48 (61.54)	0.625	2.174
10	73	46 (63.01)	27 (36.99)	1.704	6.490
11	69	29 (42.03)	40 (57.97)	0.725	0.608
12	57	26 (45.61)	31 (54.39)	0.839	0.021
13	45	21 (46.67)	24 (53.33)	0.875	0.002
14	49	23 (46.94)	26 (53.06)	0.885	0.005
15	29	15 (51.72)	14 (48.28)	1.071	0.076
16	38	12 (31.58)	26 (68.42)	0.462	3.224
17	22	12 (54.55)	10 (45.45)	1.200	0.206
18	22	7 (31.82)	15 (68.18)	0.467	1.572
19–20	23	13 (56.52)	10 (43.48)	1.300	0.066
21–24	27	13 (48.15)	14 (51.85)	0.929	0.091

N = number of sexed newborns. χ^2 test, adjusted after Yates, two-tailed. No deviations from the mean sex ratio are statistically significant ($p > 0.05$), excepting in 10 year old females, which tended to bear more sons than daughters ($0.05 > p > 0.01$). However, the 9 year old females showed the opposite (though statistically insignificant) tendency and after combining the two years together, no more deviation was apparent (76♂ : 75♀; $\chi^2_{adj} = 0.397$; n.s.). Such seeming statistical deviations are expected to occur on statistical grounds (Hill 1985).

Table 3. **Relation between the secondary sex ratio and paternal age (at foal's birth) in *Equus przewalskii*, based on the offspring of 113 stallions**

Age (Year)	N	N♂ (% ♂)	N♀ (% ♀)	N♂/N♀	χ^2_{adj}
3	8	2 (25.00)	6 (75.00)	0.333	0.853
4	34	16 (47.06)	18 (52.94)	0.889	0.013
5	79	38 (48.10)	41 (51.90)	0.927	0.001
6	96	47 (48.96)	49 (51.04)	0.959	0.030
7	101	48 (47.52)	53 (52.48)	0.906	0.009
8	91	42 (46.15)	49 (53.85)	0.857	0.034
9	108	58 (53.70)	50 (46.30)	1.160	1.398
10	93	43 (46.24)	50 (53.76)	0.860	0.023
11	76	30 (39.47)	46 (60.53)	0.652	1.681
12	66	25 (37.88)	41 (62.12)	0.610	0.358
13	56	33 (58.93)	23 (41.07)	1.435	0.420
14	49	22 (44.90)	27 (55.10)	0.815	0.053
15	40	19 (47.50)	21 (52.50)	0.905	0.023
16	38	17 (44.74)	21 (55.26)	0.810	0.035
17	32	14 (43.75)	18 (56.25)	0.778	0.065
18	32	14 (43.75)	18 (56.25)	0.778	0.065
19	25	15 (60.00)	10 (40.00)	1.500	0.419
20	26	13 (50.00)	13 (50.00)	1.000	0.003
21	22	12 (54.55)	10 (45.45)	1.200	0.196
22	16	8 (50.00)	8 (50.00)	1.000	0.003
23–27	18	10 (55.56)	8 (44.44)	1.250	0.197

N = number of sexed newborns. χ^2 test, adjusted after Yates, two-tailed. No deviations from expected distributions are statistically significant ($p > 0.05$).

Table 4. **Relation between the secondary sex ratio and parity in *Equus przewalskii***

Birth sequence	N	N♂ (% ♂)	N♀ (% ♀)	N♂/N♀	χ^2_{adj}
1	260	125 (48.08)	135 (51.92)	0.926	0.021
2	195	99 (50.77)	96 (49.23)	1.031	0.738
3	158	81 (51.27)	77 (48.73)	1.052	0.780
4	122	49 (40.16)	73 (59.84)	0.671	2.307
5	100	46 (46.00)	54 (54.00)	0.852	0.035
6	85	37 (45.12)	45 (54.88)	0.822	0.376
7	60	31 (51.67)	29 (48.33)	1.069	0.277
8	46	24 (52.17)	22 (47.83)	1.091	0.245
9	33	15 (45.45)	18 (54.55)	0.833	0.003
10	21	8 (38.10)	13 (61.90)	0.615	0.736
11–15	32	14 (43.75)	18 (56.25)	0.778	0.175

N = number of sexed newborns. χ^2 test, adjusted after Yates, two-tailed. No deviations from the mean sex ratio are statistically significant ($p > 0.05$).

Effect of birth sequence

Sex sequences in individual families were investigated in man only so far, where they were found to be random in several studies (Renkonen 1956; Edwards 1961, 1962; Loyd and Gray 1969) and non-random in other ones (Schützenberger 1949, 1950; Gray and Morrison 1974). No deviation from randomness was revealed in Przewalski horses, where sex sequences were studied in families of 122 females with 4–15 foals ($\varepsilon = 0.184$, $p > 0.1$; non-parametric run test after Wald and Wolfowitz 1940; cf. Klat 1983).

Effect of the female's predisposition

The female's predisposition to bear either more daughters or more sons can be detected by an analysis of the sex ratio distribution in litters or families (sibships). The expected statistical distribution of the sex ratio within litters or families is the binomial one (EDWARDS 1960, 1962; HARMSEN and COOKE 1983). The randomness of the sex ratio distribution in litters or families was corroborated in Przewalski horses (this study,

Table 5. **Sex ratio distribution in sibships of *Equus przewalskii***

Sibship size	No. of litters	♂:♀	No. of litters observed		No. of litters expected	χ^2
2	195	2:0	41		43.89	0.673
		1:1	103		97.25	
		0:2	51		53.87	
3	160	3:0	22		18.27	1.959
		2:1	51		58.13	
		1:2	65		61.66	
		0:3	22		21.80	
4	122	4:0	5		6.34	3.358
		3:1	32		27.76	
		2:2	39		45.56	
		1:3	39		33.24	
		0:4	7		9.10	
5	100	5:0	3	16	9.99	5.643
		4:1	13			
		3:2	22		24.55	
		2:3	37		34.47	
		1:4	21		24.19	
		0:5	4		6.79	
6	80	6:0	1	7	7.01	4.062
		5:1	6			
		4:2	16		16.84	
		3:3	18		24.81	
		2:4	27		20.57	
		1:5	10	12	10.77	
		0:6	2			
7	59	7:0	0	11	10.42	0.521
		6:1	2			
		5:2	9			
		4:3	16		14.89	
		3:4	16		16.97	
		2:5	10		11.61	
		1:6	4	6	5.13	
		0:7	2			
8	45	8:0	0	4	5.43	3.429
		7:1	1			
		6:2	3			
		5:3	9		9.05	
		4:4	15		12.23	
		3:5	9		10.58	
		2:6	7	9	7.73	
		1:7	2			
		0:8	0			

χ^2 test, two-tailed. No deviations from expected distributions are statistically significant ($p > 0.05$).

Tab. 5), dairy cattle *Bos taurus* (Gray and Hurt 1979), Siberian tigers *Panthera tigris altaica* (Mlíkovský 1985) and in several studies on man (Edwards and Fraccaro 1958, 1960; Gray and Morrison 1974; Gray and Bortolozzi 1977). On the other hand, some controversial indications exist that the sex ratio distribution in litters or families deviates from the binomial one in man (Geissler 1889; Edwards 1958), coypus (Gosling 1986a), domestic pigs (Gray and Katanbaf 1985) and in several other species of domestic mammals (Gini 1951; James 1975).

Effect of the female's body condition

Direct data on body condition of pregnant Przewalski mares were not available, but Trivers and Willard (1973) have assumed that in large mono- or oligotocous mammals, the female's body condition is higher when the female has skipped reproduction in the foregoing year. Using this measure, no effect of the female's body condition on the secondary sex ratio of that female's offspring was detected in Przewalski horses (Tab. 6) but, using another measure, Skogland (1986) revealed this effect in reindeer *Rangifer tarandus*.

Table 6. **Relation between the secondary sex ratio and reproductive effort (measured as number of foals born to 3–6 year old mares) in *Equus przewalskii***

No. of foals	N	N♂ (% ♂)	N♀ (% ♀)	N♂/N♀	χ^2_{adj}
1	60	33 (55.00)	27 (45.00)	1.222	0.409
2	119	55 (46.22)	64 (53.78)	0.859	0.004
3	126	60 (47.62)	66 (52.38)	0.909	0.016
4	16	7 (43.75)	9 (56.25)	0.778	0.032

Mares which died before 6 year old were excluded from the analysis. N = number of sexed newborns. χ^2 test, adjusted after Yates, two-tailed. No deviations from the mean sex ratio are statistically significant ($p > 0.05$).

Seasonal variations

There is a distinct, though extended, foaling season in captive Przewalski horses in the Palearctic (Mohr and Volf 1984), where 1103 of the 1115 registered Przewalski foals were born. Hence, it could by hypothesized that the secondary sex ratio will show some seasonal variation. However, no such variation was detected (Tab. 7). Baumgartner (1985), who studied the same relationship in domestic hens *Gallus gallus* f. domestica, has found such a variation in one of the two strains he studied, but not in the other one. On the other hand, a strong seasonal variation in the secondary sex ratio was found in grey seals *Halichoerus grypus* (Coulson and Hickling 1961) and in captive coypus (Gosling 1986a).

Annual variations

Year to year variations in the secondary sex ratio were reported for a number of mammalian species, including, for example, American buffalos *Bison bison* (McHugh 1959), European bisons (Koročkina 1968) and water buffalos *Bubalus bubalis* (Fischer 1966; Coswami and Nair 1968). However, no such variation was observed in Przewalski horses (this study, Tab. 8).

Table 7. **Relation between the secondary sex ratio and season in *Equus przewalskii***

Month	N	N♂ (% ♂)	N♀ (% ♀)	N♂/N♀	χ^2_{adj}
I	17	9 (52.94)	8 (47.06)	1.125	0.028
II	15	8 (53.33)	7 (46.67)	1.143	0.025
III	35	20 (57.14)	15 (42.86)	1.333	0.843
IV	148	67 (45.27)	81 (54.73)	0.827	0.328
V	358	176 (49.16)	182 (50.84)	0.967	0.162
VI	260	119 (45.77)	141 (54.23)	0.844	0.416
VII	123	56 (45.53)	67 (54.47)	0.836	0.202
VIII	55	28 (50.91)	27 (49.09)	1.037	0.092
IX	41	20 (48.78)	21 (51.22)	0.952	0.003
X	27	15 (55.56)	12 (44.44)	1.250	0.357
XI	11	5 (45.45)	6 (54.55)	0.833	0.018
XII	13	6 (46.15)	7 (53.85)	0.857	0.022

N = number of sexed newborns. χ^2 test, adjusted after Yates, two-tailed. No deviations from the mean sex ratio are statistically significant ($p > 0.05$).

Table 8. **Temporal changes of the secondary sex ratio in *Equus przewalskii***

Period	N	N♂ (% ♂)	N♀ (% ♀)	N♂/N♂	χ^2_{adj}
1901–10	13	5 (38.46)	8 (61.54)	0.625	0.165
1911–20	32	13 (40.63)	19 (59.37)	0.684	0.423
1921–30	36	15 (41.67)	21 (58.33)	0.714	0.343
1931–40	38	23 (60.53)	15 (39.47)	1.533	1.938
1941–50	25	10 (40.00)	15 (60.00)	0.667	0.352
1951–60	69	31 (44.93)	38 (55.07)	0.816	0.143
1961–65	90	45 (50.00)	45 (50.00)	1.000	0.083
1966–70	104	58 (55.77)	46 (44.23)	1.261	2.256
1971–75	162	71 (43.83)	91 (56.17)	0.780	0.934
1976–80	297	138 (46.46)	159 (53.54)	0.868	0.200
1981–83	246	124 (50.41)	122 (49.59)	1.016	0.509

N = number of sexed newborns. χ^2 test, adjusted after Yates, two-tailed. No deviations from the mean sex ratio are statistically significant ($p > 0.05$).

Discussion

Whether adaptive adjustment of the secondary sex ratio occurs in birds and mammals is still inconclusive (Williams 1979; Charnov 1982; Clutton-Brock and Albon 1982), because the relevant data are highly controversial. Since many factors may directly or indirectly affect the secondary sex ratio in higher vertebrates, it is favorable to study its variations experimentally (e.g., McClure 1981; Myers et al. 1985; Labov et al. 1986) and/or to select for the study such species or populations which are naturally independent of some of the possible factors (e.g., Rutberg 1986). As shown above, captive Przewalski horses are suitable for such a kind of research. Despite that, none of the investigated factors, viz. maternal age, paternal age, parity, birth sequence, female's predisposition, female's body condition, season and year, proved effective.

To conclude, nothing was found in the variations of the secondary sex ratio in the Przewalski horse in support of the Trivers and Willard's (1973) sex adjustment hypothesis. However, it should be noted at the same time that two other important factors were not investigated in the present study, particularly the effect of the time of fertilization

within the estrus cycle (JAMES 1976, 1983; VERME and OZOGA 1981) and the effect of the social status of the female in the herd (SILK et al. 1981; SIMPSON and SIMPSON 1982; CLUTTON-BROCK 1982; CLUTTON-BROCK et al. 1984, 1986). Hence, the results reached, though not supporting the TRIVERS and WILLARD's (1973) hypothesis, cannot be used as a proof of its incorrectness.

Zusammenfassung

Das sekundäre Geschlechterverhältnis beim Przewalski-Pferd, Equus przewalskii (Mammalia: Equidae)

Das sekundäre Geschlechterverhältnis, seine Verteilung in Familien und die Beziehungen zwischen dem sekundären Geschlechterverhältnis und dem Alter von Mutter und Vater, der Parität, Geburtsfolge, Jahreszeit und Jahr wurden bei Przewalski-Pferden untersucht. Die Verteilung des Geschlechterverhältnisses wich von einer Binomialverteilung nicht signifikant ab. In dem sekundären Geschlechterverhältnis wurden keine Variationen entdeckt. Es wich weder bei Przewalski-Pferden noch bei anderen Perissodactylen signifikant von 1:1 ab.

Diese Angaben unterstützen weder die Theorie, daß die Weibchen das Geschlecht ihrer Nachkommen beeinflussen können, noch widersprechen sie ihr direkt.

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Z. Säugetierkunde 53 (1988) 102–107
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ISSN 0044-3468

The karyotype of the European roe deer *(Capreolus capreolus* L.)

By S. Herzog

Receipt of Ms. 26. 1. 1987

Abstract

The karyotype of the European roe deer (*Capreolus capreolus* L.) is described by means of G- and C-banding techniques. A standardized idiogram (diagram, ordering of the chromosomes and designation of the bands) is proposed for the species *Capreolus capreolus* L., using the idiogram of the investigated Central European animals as an example.

Introduction

Previous investigations on the karyotype of *Capreolus capreolus* L. used orcein staining (Gustavsson 1965; Amrud and Nes 1966; Herzog and Höhn 1967; Wurster and Benirschke 1967; Gustavsson and Sundt 1968; Hsu and Benirschke 1968).

A chromosone number of 2n = 70, XX resp. XY was found. All 68 autosomes are designated as acrocentric, the X-chromosome submetacentric and the Y-chromosome subtelocentric. Amrud and Nes (1966) call the Y "apparently submetacentric".

A supernumerary submetacentric chromosome was detected by Herzog and Höhn (1967) in one specimen. The authors explained this phenomenon by a double trisomy, occurring as a centric fusion. More recently, banding techniques which allow to differentiate between single chromosomes were used by Neitzel (1982) for the investigation of the Siberian roe deer (subspecies *Capreolus capreolus pygargus*). She studied three specimens and found a chromosome number between 2n = 76 and 80, dependent on a varying number of microchromosome pairs. Similar results have been obtained by Sokolov et al. (1978), Stubbe and Passarge (1979), and Stubbe (1979), using orcein staining techniques.

In the European roe deer, a karyotype analysis by means of modern banding techniques as well as a systematic description of the bands of each chromosome in accordance with an international standard is still lacking. The purpose of the present paper is to study the karyotype of the Central European roe deer by means of G- and C-banding techniques and to propose an idiogram, thereby describing the single chromosomes in accordance with the International System for Human Cytogenetic Nomenclature (ISCN 1985), to set up a basis for further investigations, especially on homologisation of karyotypes between different taxa and studies concerning karyotype evolution.

Material and methods

In order to obtain the metaphase chromosomes, tissue cultures (kidney, skeletal muscle and testes) of 69 specimens from Hessen (Bundesrepublik Deutschland) were laid out using standard culture techniques. The metaphase chromosomes were studied by modified G- and C-banding techniques (Sumner et al. 1971; Seabright 1972) and photographed with a 1000-fold magnification under oil immersion. In order to obtain a homogeneous degree of condensation in the G-banded chromosomes, only metaphases exhibiting nine G-bands on the X-chromosome (three on the short arm and six on the long arm) were taken into consideration.

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Fig. 1. G-banded idiogram of a male European roe deer (*Capreolus capreolus* L.)

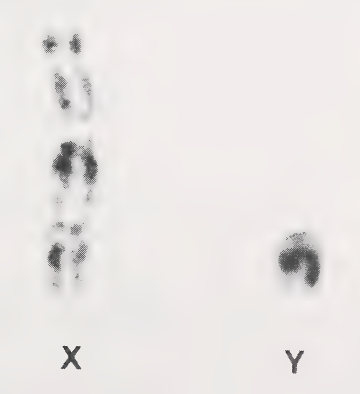


Fig. 2. Gonosomes (X and Y) of the European roe deer (*Capreolus capreolus* L.)

Table. **Arm-length-ratio in the X-chromosome of *Capreolus capreolus* L., revealed by measurements of 26 haploid chromosome sets**

Arm	relative length* ($\bar{x}$)	standard deviation (s_x)
p-arm	2.19	0.30
q-arm	3.00	0.39

* as percentage of the total length of the haploid autosome set.

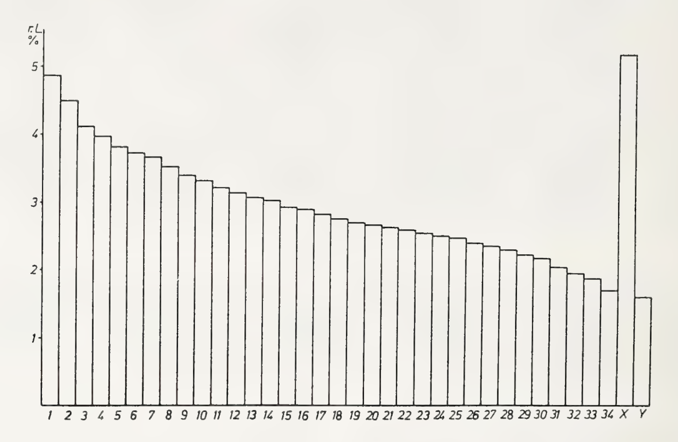


Fig. 3. Chromosome length in *Capreolus capreolus* L. (r. L. = relative length in percent of the total haploid autosome set)

Results

The somatic, diploid chromosome set of all 69 animals studied consists of 70 chromosomes, namely 68 autosomes and two gonosomes (2n = 70, XX resp. XY; figs. 1 and 2).

Measurements of the chromosome lengths show that all autosome pairs and the Y-chromosome are telocentric (according to the terminology of Nagl 1980) with an arm-length ratio less than 1:4. The female gonosome is subtelocentric (see table). Using high-quality preparations, short (p-)arms are obvious in all telocentric chromosomes. Thus, the Nombre fondamental (N. F.) is 140 if these short arms are taken into account, whereas it is 72 in the female and 71 in the male if the short p-arms are neglected.

The autosomal N. F. (N. F.a) is 68 resp. 136 in both male and female.

The centromeric index (c.i.) is not useful for the characterization of the chromosomes, because the p-arms of the telocentrics are not unequivocally measurable and chromosome lengths of the related chromosome pairs show only slight differences (fig. 3), mostly less than the standard deviation of the chromosome length of the relevant pairs.

Therefore it seems indispensable to use banding patterns as a tool for identification of the individual homologous chromosomes. Fig. 4 shows a proposal for the idiogram of *Capreolus capreolus* L. The bands and landmarks are drawn from the photos of the chromosomes of all 69 deer following the ISCN (1985). All autosomes exhibit distinct C-bands of different size. The euchromatin of a single autosome becomes stained over the whole length after C-banding treatment (facultative heterochromatin, fig. 5). The gonosomes show no visible C-bands, but in the female, one of the two X-chromosomes also exhibits facultative heterochromatin (sexchromatin), a phenomenon which is well known in other species, especially mammals. The occurrence of facultative heterochroma-

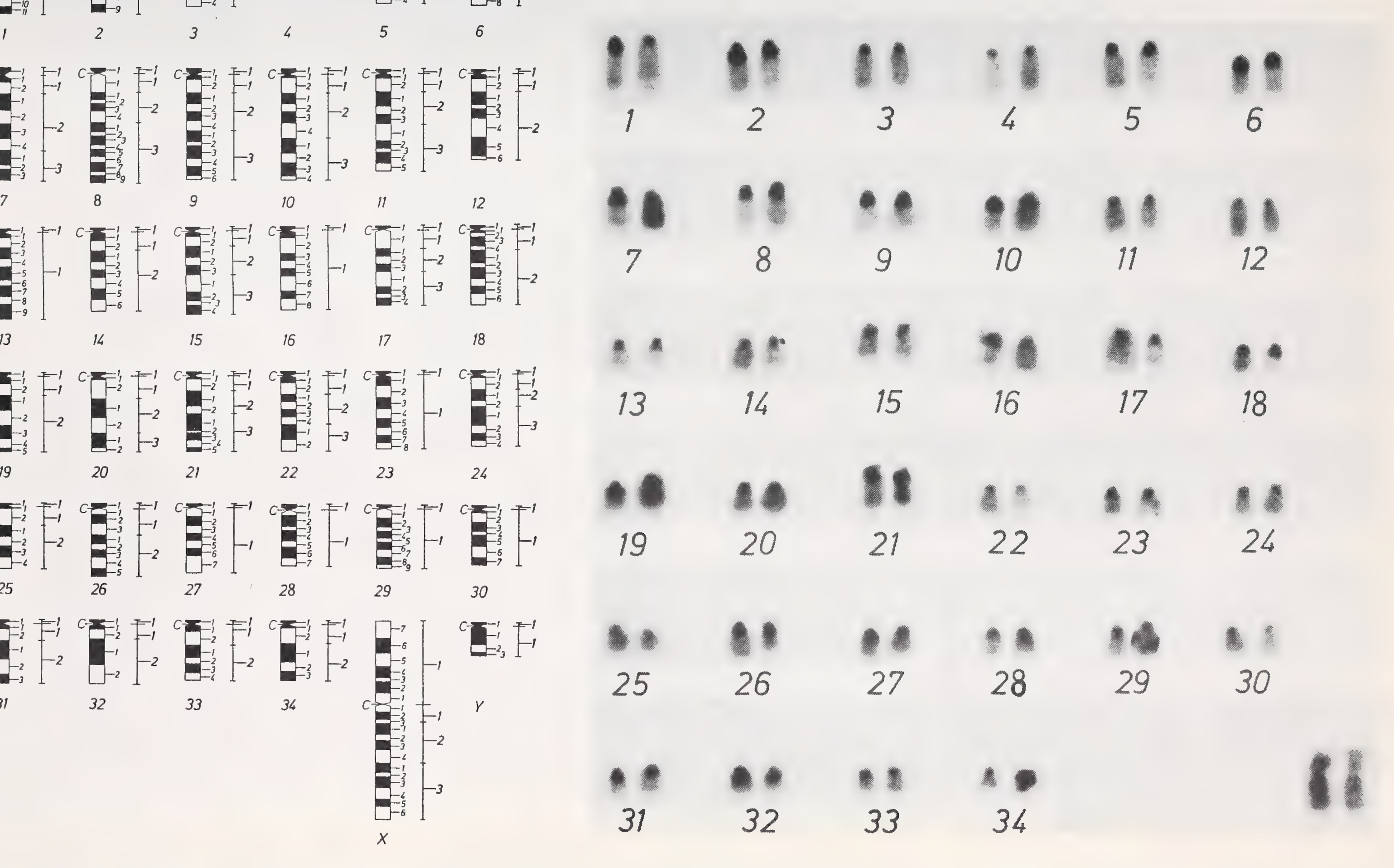


Fig. 4 (left). Proposition for a standard idiogram of *Capreolus capreolus* L. following the ISCN (1985): big numbers = landmarks, small numbers = bands, C = centromere. – *Fig. 5 (right).* C-banded idiogram of a female European roe deer (*Capreolus capreolus* L.)

tin in originally euchromatic regions is interpreted usually by the inactivation of one chromosome in a pair for gene dosis compensation (for a review see Nagl 1980).

Discussion

The present investigation on the karyotype of European roe deer confirms the results of Gustavsson (1965), Herzog and Höhn (1967), Wurster and Benirschke (1967), Gustavsson and Sundt (1968) as well as Hsu and Benirschke (1968) as regards the chromosome number of *Capreolus capreolus.* The Siberian roe deer *(Capreolus capreolus pygargus)* also shows the characteristic chromosome number of 2n = 70 and, in addition, an unstable number of microchromosomes (Sokolov et al. 1978; Stubbe and Passarge 1979; Stubbe 1979; Neitzel 1982). Neitzel (1982) assumes that the microchromosomes show regular mitotic segregation, because their number is constant within each investigated individual. A supernumerary submetacentric chromosome detected by Herzog and Höhn (1967) in one specimen of roe deer from Hessen (Bundesrepublik Deutschland) could not be found in the present investigation nor is it mentioned by other authors, which means that such a chromosome mutation is either uncommon in the European roe deer or it is lethal at an early ontogenetic stage. With respect to the form of the chromosomes, the previous investigations could be confirmed only partially, because the short p-arms are not described in these papers. In consequence, the autosomes are not acro- but telocentric, according to the terminology given by Nagl (1980). Moreover, the Y-chromosome is also telocentric and not subtelocentric or submetacentric as assumed by previous authors. The X-chromosome was identified as subtelocentric. The photos of the orcein stained chromosomes given in the above mentioned first papers about the karyotype of roe deer suggest that the differences in the morphology of the gonosomes, especially the Y-chromosome, might be explainable by the unconsistent use of the terminology. However, it also may be possible that Y chromosomes with p-arms longer than those of the autosomes are existing, but there is no certain indication. Further investigations on this question should be carried out using electron microscopy. Photos of G-banded chromosomes 1 to 16 are shown by Neitzel (1982) for the Siberian roe deer *(Capreolus capreolus pygargus).* Although these chromosomes seem to be stained at a more condensed stage, the landmark patterns are similar to those of the investigated animals from Hessen. This indicates that there might be no considerable differences between the banding patterns of chromosomes 1 to 16 of the deer from Central Europe and from Siberia. Moreover, the other autosomes also seem to be similar in the Siberian and the Central European roe deer as regards their G-banding pattern, which is described by Neitzel (1982), who compares the karyotypes of different Cervidae, including the Siberian roe deer, with a karyotype assumed to be ancestral for the Cervidae.

The C-banding patterns described by Neitzel (1982) are similar to those revealed in the present investigation: She also found C-bands in each autosome, but not distinct C-bands in the gonosomes. The microchromosomes of the Siberian roe deer are described as fully heterochromatic. Banding techniques, such as G-banding, and a standard basis for description of the single chromosomes, such as the ISCN (1985), should enable the investigator to identify nearly all chromosomes reliably and appear to be useful for homologisation of the karyotypes between different taxonomic groups as well as for studies on karyotype evolution or for gene mapping. Moreover, C-banding is very important, especially for investigations on karyotype evolution. For studies on population genetics in this species, C-banding may become useful if any C-band polymorphisms can be found and identified as markers by genetic analysis.

Acknowledgements

The author is very grateful to Prof. Dr. A. Herzog and Dr. Henni Höhn, Fachgebiet Veterinärmedizinische Genetik und Zytogenetik, Institut für Tierzucht und Haustiergenetik der Universität Gießen, for the help and advice during the experimental work. The studies were supported financially by the Hessischer Minister für Landwirtschaft und Umwelt.

Zusammenfassung

Der Karyotyp des europäischen Rehes (Capreolus capreolus L.)

Der Karyotyp des mitteleuropäischen Rehes wurde mittels G- und C-Bandentechnik beschrieben. Ein standardisiertes Idiogramm (Anordnung der Chromosomen und Bezeichnung der Banden) wurde für die Species *Capreolus capreolus* L. am Beispiel des Idiogramms der untersuchten mitteleuropäischen Tiere vorgeschlagen.

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Z. Säugetierkunde 53 (1988) 108–123

ISSN 0044-3468

Osteomorphological features of the appendicular skeleton of African buffalo, *Syncerus caffer* (Sparrman, 1779) and of domestic cattle, *Bos primigenius* f. taurus Bojanus, 1827

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Receipt of Ms. 10. 11. 1986

Abstract

Studied the osteomorphological differences between the appendicular skeleton of African buffalo *(Syncerus caffer)* and domestic cattle (*Bos primigenius* f. taurus). Osseous remains derived from these large bovids, frequently found in African Holocene archaeological sites, can not be distinguished easily.

A key has been developed to meet this recurrent problem and a number of diagnostic, osteomorphological features are established, which allow a distinction between the two species. Only a few of the smaller carpal and tarsal bones can not be separated yet. In general, osteomorphological differences are more constant than osteometrical differences and therefore seem more useful. Most of the ostemorphological criteria, established for domestic cattle can also be used to identify remains of their wild ancestor, the aurochs *(Bos primigenius).*

Introduction

The following study was undertaken within the frame of our Ph. D. research on faunal remains from archaeological sites in Central and Eastern Sudan (cf. Marks et al. 1985; Peters 1986a, 1986b). During this archaeozoological analysis, we were confronted with the fact that the majority of our samples was dominated by osseous remains from members of the family Bovidae, ranging in size from the small oribi *(Ourebia ourebi)* up to the large buffalo *(Syncerus caffer).* Because of (1) the diversity of bovid species within these collections (up to 20 species or more), (2) their mixed composition with domesticated and wild bovids and (3) the pronounced fragmentation of the bone material, their identification presented considerable problems. The literature available on African bovid osteology focuses mainly on the morphology of the skull, including the teeth (e.g. Arambourg 1947; Gentry 1964, 1967, 1978; Stöckmann 1975; Van Neer 1981 and others). Postcranial skeletons, however, are poorly known, for descriptions of their osteomorphological characteristics, useful to the archaeozoologist, are quite rare (Arambourg 1947; Gentry 1967; Leinders and Sondaar 1974; Oboussier and Ernst 1977; Leinders 1979; Van Neer 1981; Gabler 1985; Walker 1985). To solve partly our identification problems, we carried out a few osteomorphological studies on recent and fossil postcranial material of African and other bovids. The choice of the species considered in these contributions is conditioned by an important question concerning the life style of prehistoric man: are domesticated animals present in our collections or not? Therefore, this first analysis deals with the osteomorphology of two very large bovids, of which, until now, the postcranial skeleton could not be separated accurately: the African buffalo, *Syncerus caffer* and domestic cattle, *Bos primigenius* f. taurus.

Within the descriptive part, we include several distinctive features already recorded by other authors in earlier publications (Dottrens 1946; Gentry 1967) or reports (Payne s.d.). To distinguish between the phalanges of the fore and hind limbs of cattle, we used

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some of the criteria established by DOTTRENS (1946). As to the work by GENTRY (1967), we do not agree with the conclusions concerning the distinction between certain skeletal elements of *Bos* and *Syncerus*. We suspect that the small size of the sample used by this researcher may be responsible for our differences of opinion.

In the course of our study, we also collected an impressive amount of osteometrical data, which enabled us to calculate many indices. This information has not been included here for practical reasons, but it can be obtained from the author at the address listed below. Both these osteometrical data and the ones summarized here will be available soon in an extensive, technical paper (PETERS 1986c). This paper is distributed on a very limited scale; therefore we thought it useful to publish separately the following short article.

Material and methods

The following results are based on a detailed analysis of the appendicular skeleton of the two species involved. As to the African buffalo *(Syncerus caffer)*, 25 adults, including both sexes, were carefully examined. All three subspecies sensu HALTENORTH and DILLER (1979:95) are present: the forest buffalo *(S. c. nanus)*, the western savanna buffalo *(S. c. brachyceros)* and the savanna buffalo *(S. c. caffer)*. The specimens studied are collected from all over Africa, but mainly Zaire. They are stored in the Koninklijk Museum voor Midden-Afrika, Tervuren-Belgium; the Koninklijk Belgisch Instituut voor Natuurwetenschappen, Brussels and the British Museum (Natural History), London.

From cattle (*Bos primigenius* f. taurus), 15 adults, including both sexes and hundreds of fossil specimens collected in archaeological sites of varying ages in Europe (Neolithic to Modern Times) were examined. The recent material consists of European as well as African specimens of extant breeds. This material is stored in the institutions already mentioned, and partly in the Laboratorium voor Paleontologie and the Laboratorium voor Anatomie van de Huisdieren, both at the Rijksuniversiteit Gent.

For the osteomorphological descriptions, we have followed strictly the nomenclature proposed by the International Committee on Veterinary Gross Anatomical Nomenclature in their 'Nomina Anatomica Veterinaria' (3rd. ed., 1983). The figures were drawn by Mrs. J. BAETENS from right limb bones with the light coming from the lefthand top corner; each scale bar represents 20 mm. Note that the first and second phalanges belong to the fourth digit; the third phalanges are taken from the third digit. We did not consider the dew claws in this study.

Results

Osteomorphological features of the appendicular skeleton of African buffalo and cattle

The relevant diagnostic features are indicated by a number between brackets, which is also given on the plates. Arrows on these plates indicate morphological differences, lines refer to general differences in proportions.

Scapula

1. The position of the spina scapulae differs in the two genera. In *Bos,* the spina scapulae is slightly curved so that the acromion projects across the line of the margo cranialis when the bone is laterally viewed (pl. 1, fig. 1, char. 1). In *Syncerus* the ventral portion of the spina scapulae appears to be rather straight, so that the acromion remains within the line of the margo cranialis (pl. 1, fig. 2). As a consequence, the width ratio fossa supraspinata: fossa infraspinata is circa 1 to 3 in *Bos,* in stead of 1 to 2 or 2.5 in *Syncerus.*

2. The lateral border of the cavitas glenoidalis exhibits a medial notch in *Bos* (pl. 1, fig. 3, char. 2). In *Syncerus,* a comparable notch has been observed only once; in all other specimens it was less pronounced or even absent (pl. 1, fig. 4).

3. In *Syncerus,* the incisura glenoidalis is well developed, while in *Bos* it is almost completely absent (pl. 1, figs. 3–4, char. 3).

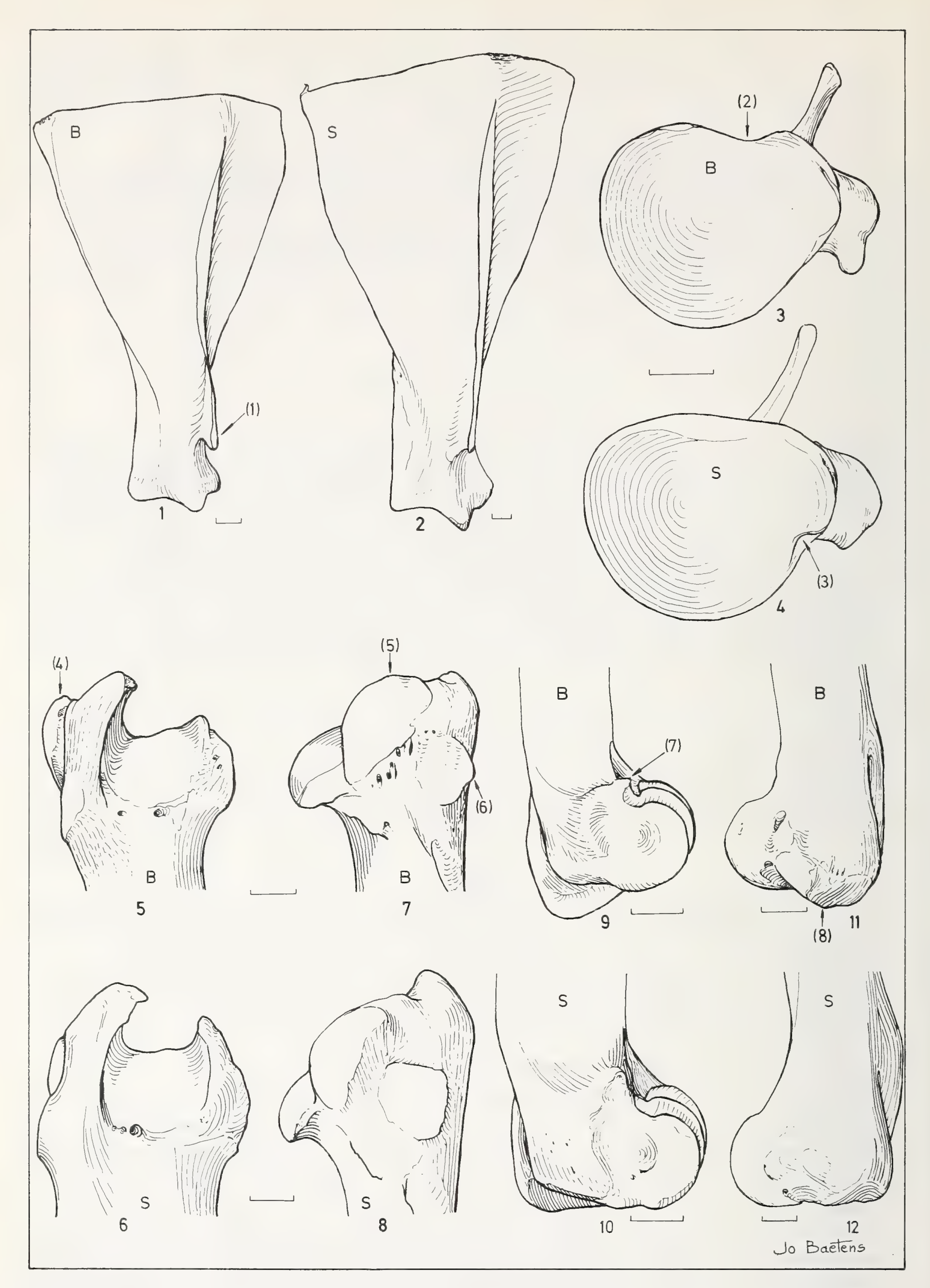


Plate 1. 1: Scapula, lateral view, *Bos primigenius* f. taurus, 2: Scapula, lateral view, *Syncerus caffer*, 3: Scapula, distal view, *Bos primigenius* f. taurus, 4: Scapula, distal view, *Syncerus caffer*, 5: Humerus, proximal extremity, cranial view, *Bos primigenius* f. taurus, 6: Humerus, proximal extremity, cranial view, *Syncerus caffer*, 7: Humerus, proximal extremity, lateral view, *Bos primigenius* f. taurus, 8: Humerus, proximal extremity, lateral view, *Syncerus caffer*, 9: Humerus, distal extremity, lateral view, *Bos primigenius* f. taurus, 10: Humerus, distal extremity, lateral view, *Syncerus caffer*, 11: Humerus, distal extremity, medial view, *Bos primigenius* f. taurus, 12: Humerus, distal extremity, medial view, *Syncerus caffer*

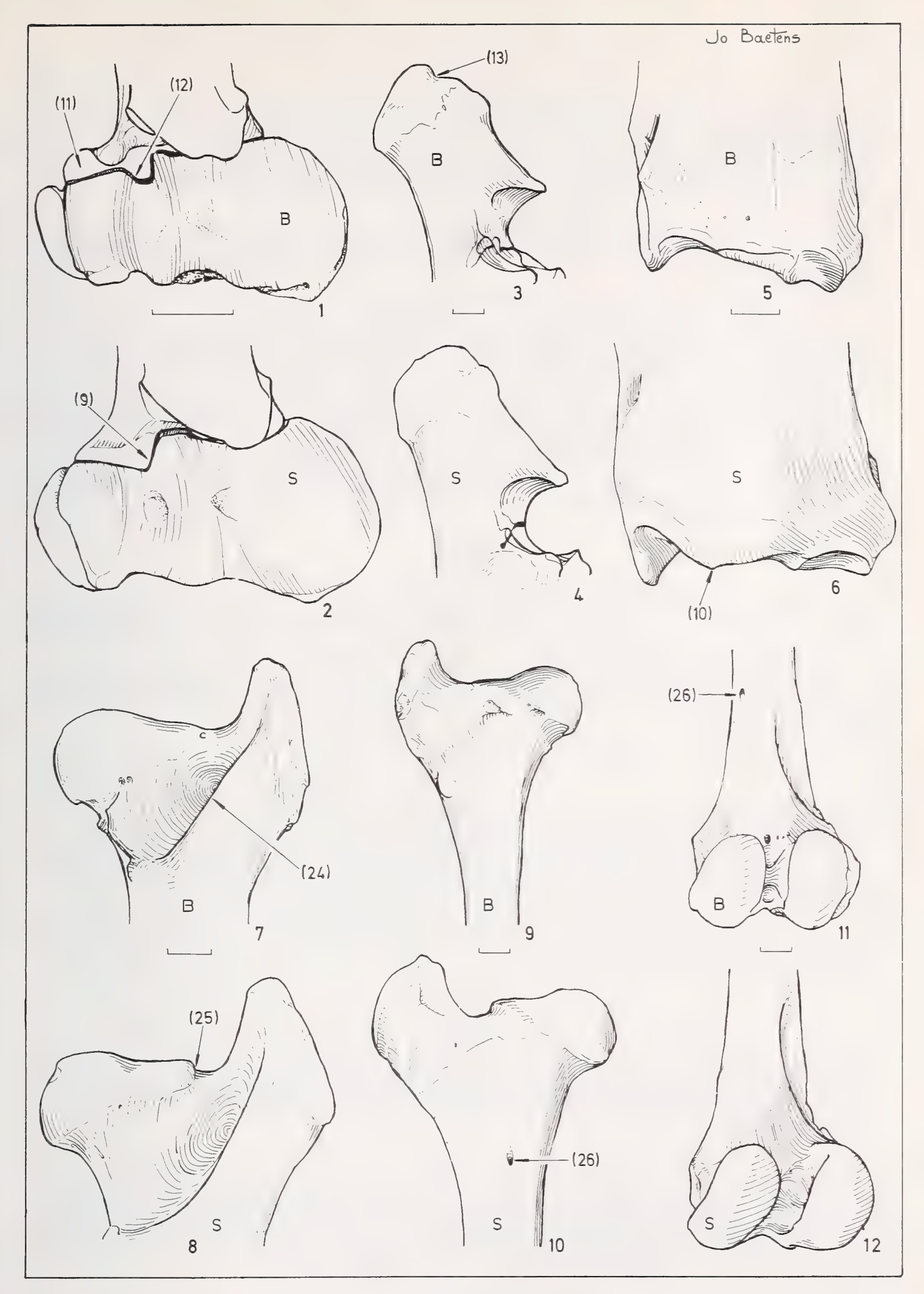


Plate 2. 1: Radius-Ulna, proximal extremity, proximal view, *Bos primigenius* f. taurus, 2: Radius-Ulna, proximal extremity, proximal view, *Syncerus caffer*, 3: Ulna, olecranon, lateral view, *Bos primigenius* f. taurus, 4: Ulna, olecranon, lateral view, *Syncerus caffer*, 5: Radius-Ulna, distal extremity, cranial view, *Bos primigenius* f. taurus, 6: Radius-Ulna, distal extremity, cranial view, *Syncerus caffer*, 7: Os femoris, proximal extremity, caudal view, *Bos primigenius* f. taurus, 8: Os femoris, proximal extremity, caudal view, *Syncerus caffer*, 9: Os femoris, proximal extremity, cranial view, *Bos primigenius* f. taurus, 10: Os femoris, proximal extremity, cranial view, *Syncerus caffer*, 11: Os femoris, distal extremity, caudal view, *Bos primigenius* f. taurus, 12: Os femoris, distal extremity, caudal view, *Syncerus caffer*

Humerus

1. The position of the pars caudalis of the tuberculum majus, relative to that of the pars cranialis differs in the two genera. In a cranial view, the pars caudalis projects more laterally compared with the pars cranialis in *Bos,* while in *Syncerus* both are lying more or less in the same plane (pl. 1, figs. 5–6, char. 4).

2. The pars caudalis of the tuberculum majus is proximally and caudally more developed in *Bos* compared with *Syncerus* (pl. 1, figs. 7–8, char. 5) (see also Gentry 1967:284-char. 71).

3. A lateral view of the humerus of *Bos* shows that the facies musculi infraspinati is well developed cranially, through which it forms a projection at the cranial side of the humerus. In *Syncerus,* this rough prominence is less pronounced and less well developed cranially (pl. 1, figs. 7–8, char. 6) (see also Gentry 1967: 284-char. 72).

4. The transition between the epicondylus lateralis humeri and the fossa radialis humeri is in *Bos* characterized by a cranioproximal, rather pointed attachment surface. In *Syncerus,* this attachment area is less pronounced (pl. 1, figs. 9–10, char. 7).

5. The epicondylus medialis is more developed distally in *Bos* compared with *Syncerus* (pl. 1, figs. 11–12, char. 8).

Radius

1. The margo caudalis of the proximal articular surface shows a different course in both genera. This is due to the differences in form and proportions of the lateral part of the incisura ulnaris (pl. 2, figs. 1–2, char. 9).

2. The portion of the margo cranialis of the facies articularis carpea, which corresponds with the dorsal border of the os carpi intermedium, extends more distally in *Syncerus* (pl. 2, figs. 5–6, char. 10).

Ulna

1. In *Bos,* the processus coronoideus lateralis is decidedly more developed laterally compared with *Syncerus* (pl. 2, figs. 1–2, char. 11).

2. In *Bos,* the incisura lateralis has a rectangular form, while in *Syncerus* this incisura is rather triangular and less well pronounced at both its dorsal and lateral side (pl. 2, figs. 1–2, char. 12).

3. The tuber olecrani exhibits in *Bos* a distinct proximal notch which is almost lacking in *Syncerus* (pl. 2, figs. 3–4, char. 13).

Ossa carpi

Os carpi radiale. 1. The ratio of the proximodistal versus dorsopalmar dimensions is different in the two genera (pl. 4, figs. 1–2, char. 14). 2. The margo medialis exhibits a slightly more angular course in *Bos* in comparison with *Syncerus* (pl. 4, figs. 3–4, char. 15) (see also Gentry, 1967: 284-char. 83).

Os carpi intermedium. 1. The margo palmaris of the facies articularis proximalis is more developed proximally in *Bos* (pl. 4, figs. 5–6, char. 16). 2. The angle between the palmar border and the (oblique) medial border of the facies articularis distalis is about 45° in *Syncerus,* while in *Bos* this angle is about 30° (pl. 4, figs. 5–6, char. 17).

Os carpi ulnare. The facies articularis medialis of the os carpi ulnare is in *Bos* much more pronounced in comparison with *Syncerus* (pl. 4, figs. 7–10, char. 18).

Os carpi accessorium. No constant osteomorphological differences were found.

Os carpale II + III. 1. In a proximal view, the habitus of the os carpale II + III is rather squarish in *Syncerus,* while in *Bos* this carpal bone looks more rectangular because of an increased mediolateral distance (pl. 4, figs. 11–12, char. 19). 2. In *Bos,* the medial articular surface is cut into two parts by a distopalmar groove. In *Syncerus,* this medial articular surface remains uniform (pl. 4, figs. 13–14, char. 20).

Os carpale IV. No constant osteomorphological differences were found.

Os metacarpale III + IV

1. The habitus of the os metacarpale III + IV differs in the two genera: relatively slender in *Bos,* while shorter, broader and rather sturdy in *Syncerus* (pl. 4, figs. 15–16, char. 21) (see partly GENTRY 1967: 282-char. 62).

2. The foramen nutricium at the palmar side of the distal extremity is well developed in *Bos,* while in *Syncerus* this foramen is reduced or even absent (pl. 4, figs. 15–16, char. 22) (see also GENTRY 1967: 282-char. 66).

3. The tuberositas ossis metacarpalis III is more pronounced in *Bos* than in *Syncerus* (pl. 4, figs. 17–18, char. 23).

Os femoris

1. The central portion of the crista intertrochanterica has a minor mediodorsal fold, which is absent in *Syncerus* (pl. 2, figs. 7–8, char. 24).

2. The caput ossis femoris merges gradually into the trochanter major in *Bos,* while in *Syncerus* the edge of the caput ossis femoris forms a clear boundary between the medial and lateral parts of the proximal extremity (pl. 2, figs. 7–8, char. 25). We agree with GENTRY (1967: 280-char. 49) that *Bos* tends to have a steeper slope on the top edge of the articular head in anterior view compared with *Syncerus,* although this feature is not distinguishable in every bone or bone fragment.

3. In *Syncerus,* a foramen nutricium is present near the proximal end of the femur. In *Bos*, a comparable foramen is located at the caudal side of the femur diaphysis near the distal end, slightly proximomedial of the fossa supracondylaris (pl. 2, figs. 9–12, char. 26).

4. The medial ridge of the trochlea ossis femoris extends more proximally in *Bos;* this trochlea is altogether more developed proximally compared with its analogue in *Syncerus* (pl. 3, figs. 1–2, char. 27).

5. The lateral ridge of the trochlea ossis femoris is more pronounced distally in *Syncerus* (pl. 3, figs. 3–4, char. 28).

Patella

The patella of *Bos* generally has, in comparison with *Syncerus,* a more slender habitus; this is partly due to a prolonged proximodistal axis (pl. 3, figs. 5–6, char. 29).

Tibia

The sulcus malleolaris lateralis is more pronounced in *Bos*. The morphology of the facies articularis malleoli is also different in the two genera (pl. 3, figs. 7–10, char. 30).

Os malleolare

The cranioproximal portion of the os malleolare of *Syncerus* is in most cases protruding proximally (pl. 4, figs. 11–12, char. 31).

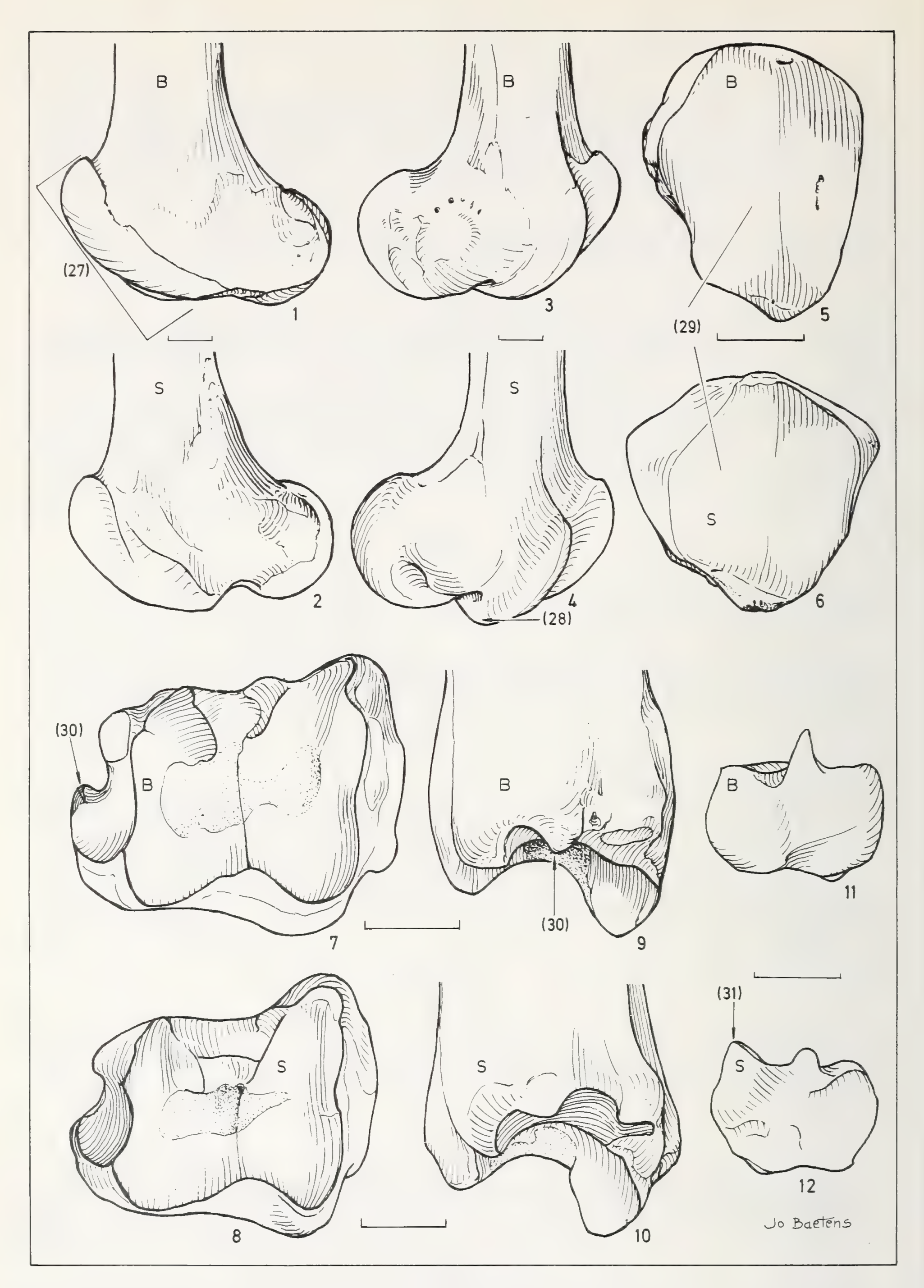


Plate 3. 1: Os femoris, distal extremity, medial view, *Bos primigenius* f. taurus, 2: Os femoris, distal extremity, medial view, *Syncerus caffer*, 3: Os femoris, distal extremity, lateral view, *Bos primigenius* f. taurus, 4: Os femoris, distal extremity, lateral view, *Syncerus caffer*, 5: Patella, caudal view, *Bos primigenius* f. taurus, 6: Patella, caudal view, *Syncerus caffer*, 7: Tibia, distal epiphysis, distal view, *Bos primigenius* f. taurus, 8: Tibia, distal epiphysis, distal view, *Syncerus caffer*, 9: Tibia, distal extremity, lateral view, *Bos primigenius* f. taurus, 10: Tibia, distal extremity, lateral view, *Syncerus caffer*, 11: Os malleolare, lateral view, *Bos primigenius* f. taurus, 12: Os malleolare, lateral view, *Syncerus caffer*

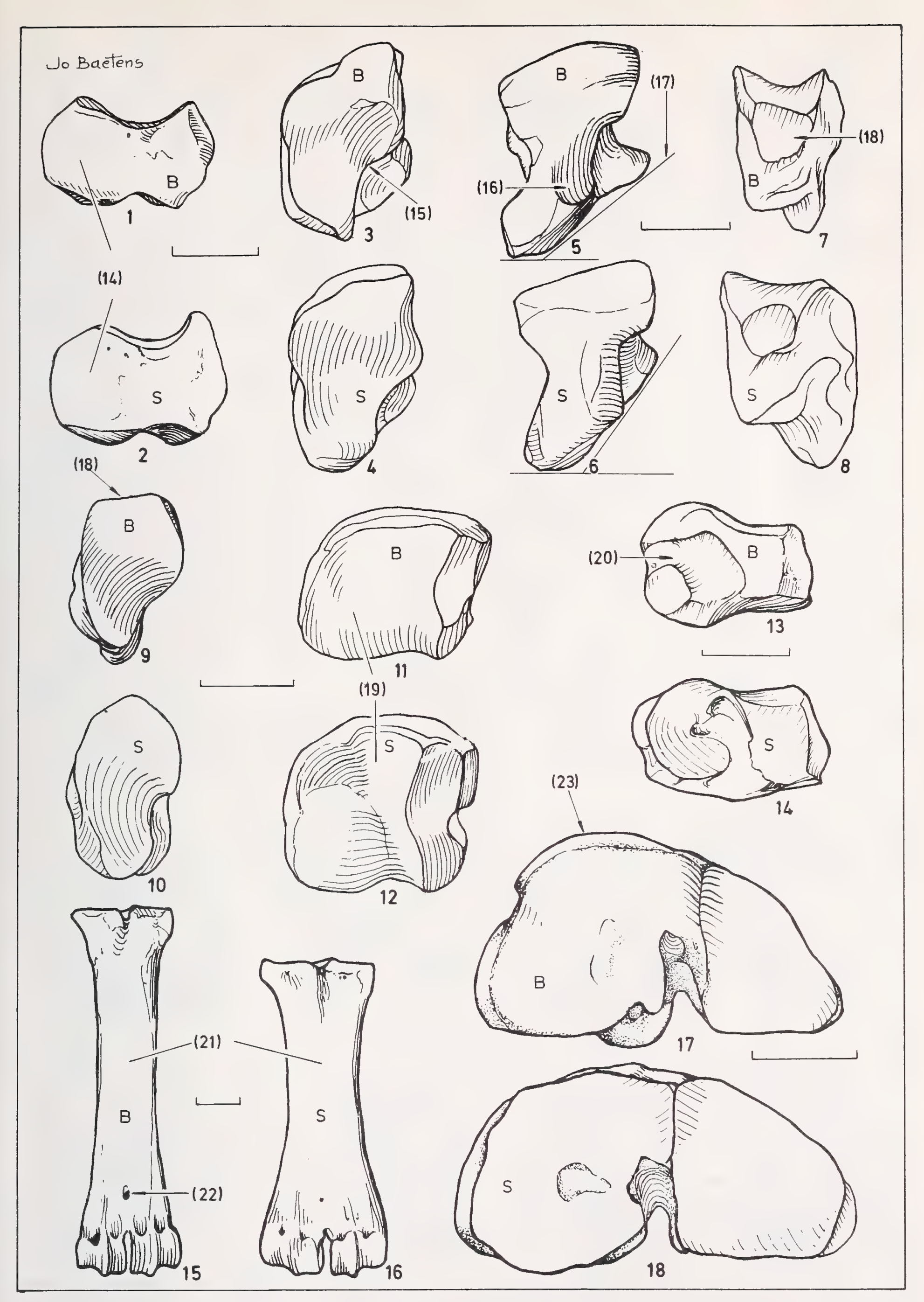


Plate 4. 1: Os carpi radiale, dorsomedial view, *Bos primigenius* f. taurus, 2: Os carpi radiale, dorsomedial view, *Syncerus caffer*, 3: Os carpi radiale, proximal view, *Bos primigenius* f. taurus, 4: Os carpi radiale, proximal view, *Syncerus caffer*, 5: Os carpi intermedium, proximal view, *Bos primigenius* f. taurus, 6: Os carpi intermedium, proximal view, *Syncerus caffer*, 7: Os carpi ulnare, dorsal view, *Bos primigenius* f. taurus, 8: Os carpi ulnare, dorsal view, *Syncerus caffer*, 9: Os carpi ulnare, proximal view, *Bos primigenius* f. taurus, 10: Os carpi ulnare, proximal view, *Syncerus caffer*, 11: Os carpale II + III, proximal view, *Bos primigenius* f. taurus, 12: Os carpale II + III, proximal view, *Syncerus caffer*, 13: Os carpale II + III, medial view, *Bos primigenius* f. taurus, 14: Os carpale II + III, medial view, *Syncerus caffer*, 15: Os metacarpale III + IV, palmar view, *Bos primigenius* f. taurus, 16: Os metacarpale III + IV, palmar view, *Syncerus caffer*, 17: Os metacarpale III + IV, proximal epiphysis, proximal view, *Bos primigenius* f. taurus, 18: Os metacarpale III + IV, proximal epiphysis, proximal view, *Syncerus caffer*

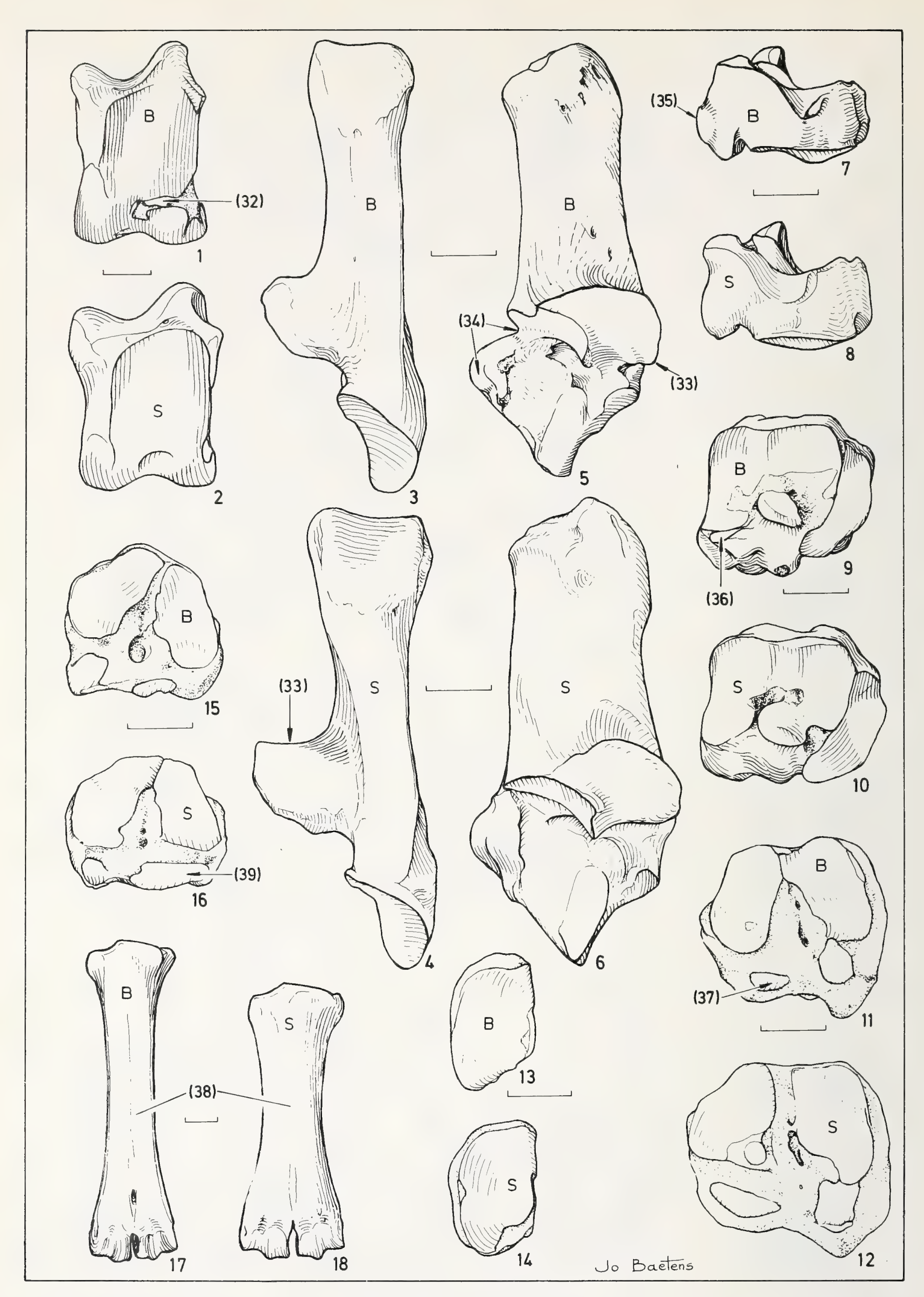


Plate 5. 1: Talus, plantar view, *Bos primigenius* f. taurus, 2: Talus, plantar view, *Syncerus caffer*, 3: Calcaneus, plantar view, *Bos primigenius* f. taurus, 4: Calcaneus, plantar view, *Syncerus caffer*, 5: Calcaneus, medial view, *Bos primigenius* f. taurus, 6: Calcaneus, medial view, *Syncerus caffer*, 7: Os centroquartale, lateral view, *Bos primigenius* f. taurus, 8: Os centroquartale, lateral view, *Syncerus caffer*, 9: Os centroquartale, proximal view, *Bos primigenius* f. taurus, 10: Os centroquartale, proximal view, *Syncerus caffer*, 11: Os centroquartale, distal view, *Bos primigenius* f. taurus, 12: Os centroquartale, distal view, *Syncerus caffer*, 13: Os tarsale II + III, proximal view, *Bos primigenius* f. taurus, 14: Os tarsale II + III, proximal view, *Syncerus caffer*, 15: Os metatarsale III + IV, proximal epiphysis, proximal view, *Bos primigenius* f. taurus, 16: Os metatarsale III + IV, proximal epiphysis, proximal view, *Syncerus caffer*, 17: Os metatarsale III + IV, dorsal view, *Bos primigenius* f. taurus, 18: Os metatarsale III + IV, dorsal view, *Syncerus caffer*

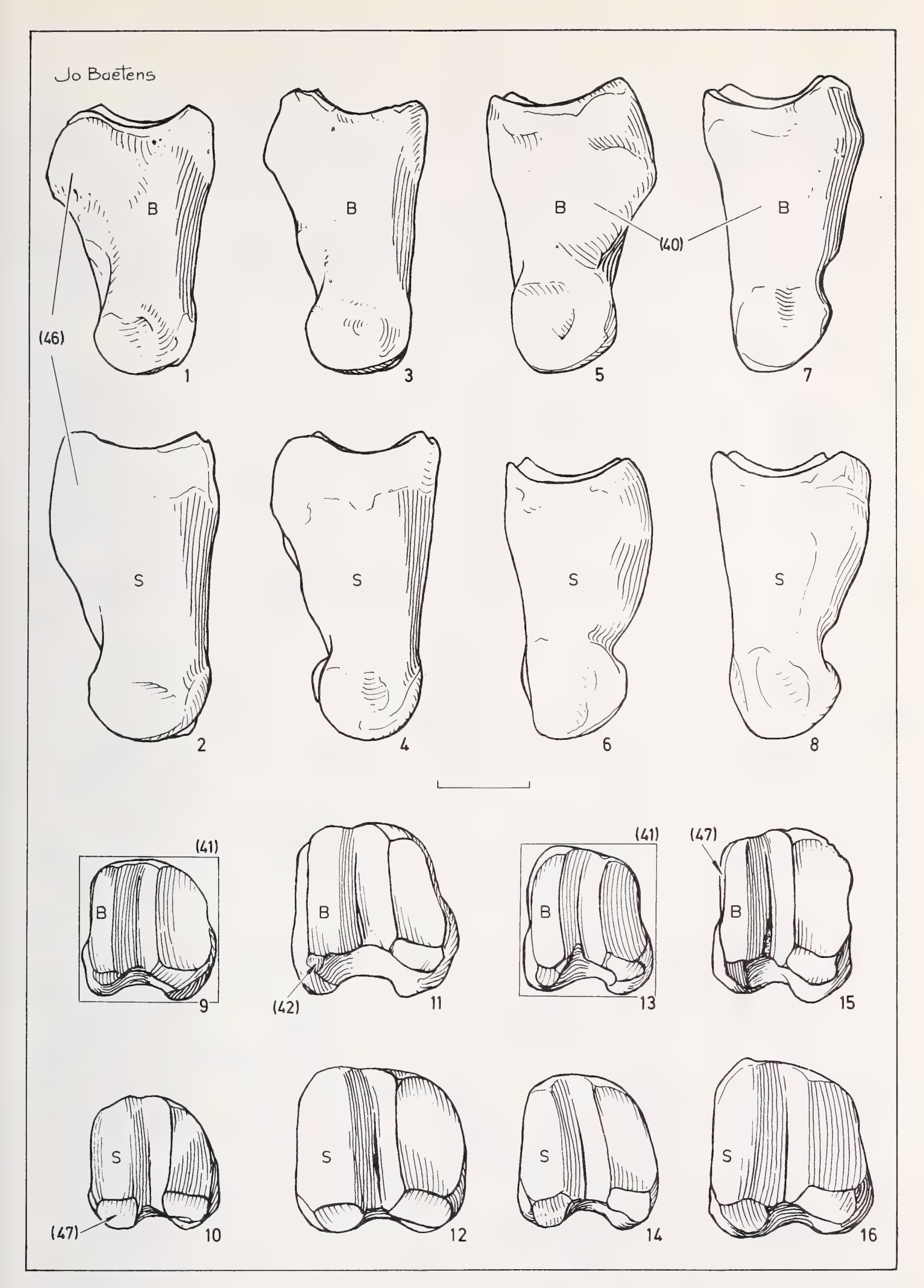


Plate 6. 1: P. proximalis manus, abaxial view, *Bos primigenius* f. taurus, 2: P. proximalis manus, abaxial view, *Syncerus caffer*, 3: P. proximalis pedis, abaxial view, *Bos primigenius* f. taurus, 4: P. proximalis pedis, abaxial view, *Syncerus caffer*, 5: P. proximalis manus, axial view, *Bos primigenius* f. taurus, 6: P. proximalis manus, axial view, *Syncerus caffer*, 7: proximalis pedis, axial view, *Bos primigenius* f. taurus, 8: P. proximalis pedis, axial view, *Syncerus caffer*, 9: P. proximalis manus (♀), proximal view, *Bos primigenius* f. taurus, 10: P. proximalis manus (♀), proximal view, *Syncerus caffer*, 11: P. proximalis manus (♂), proximal view, *Bos primigenius* f. taurus, 12: P. proximalis manus (♂), proximal view, *Syncerus caffer*, 13: P. proximalis pedis (♀), proximal view, *Bos primigenius* f. taurus, 14: P. proximalis pedis (♀), proximal view, *Syncerus caffer*, 15: P. proximalis pedis (♂), proximal view, *Bos primigenius* f. taurus, 16: P. proximalis pedis (♂), proximal view, *Syncerus caffer*

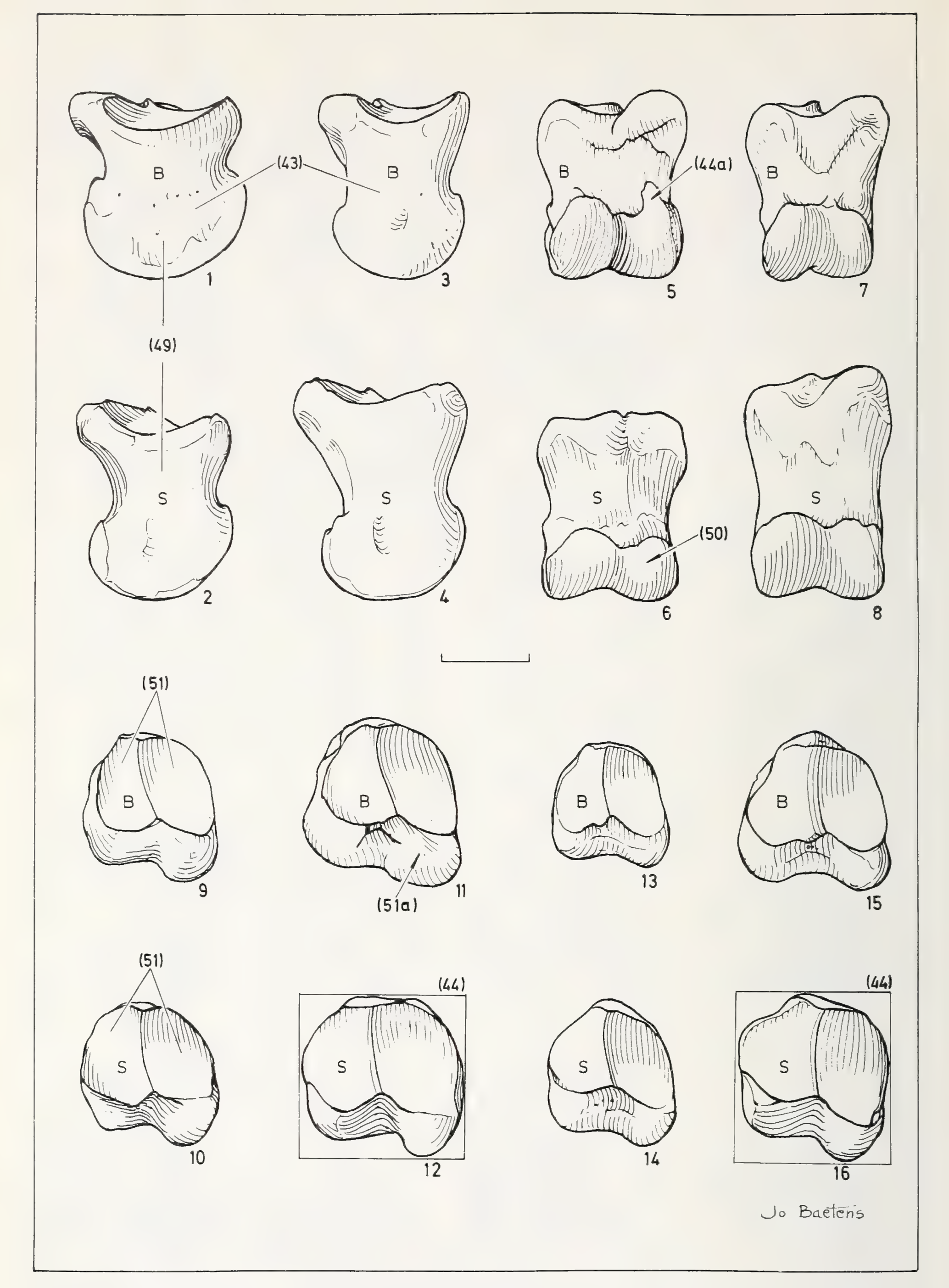


Plate 7. 1: P. media manus, abaxial view, *Bos primigenius* f. taurus, 2: P. media manus, abaxial view, *Syncerus caffer*, 3: P. media pedis, abaxial view, *Bos primigenius* f. taurus, 4: P. media pedis, abaxial view, *Syncerus caffer*, 5: P. media manus, palmar view, *Bos primigenius* f. taurus, 6: P. media manus, palmar view, *Syncerus caffer*, 7: P. media pedis, plantar view, *Bos primigenius* f. taurus, 8: P. media pedis, plantar view, *Syncerus caffer*, 9: P. media manus (♀), proximal view, *Bos primigenius* f. taurus, 10: P. media manus (♀), proximal view, *Syncerus caffer*, 11: P. media manus (♂), proximal view, *Bos primigenius* f. taurus, 12: P. media manus (♂), proximal view, *Syncerus caffer*, 13: P. media pedis (♀), proximal view, *Bos primigenius* f. taurus, 14: P. media pedis (♀), proximal view, *Syncerus caffer*, 15: P. media pedis (♂), proximal view, *Bos primigenius* f. taurus, 16: P. media pedis (♂), proximal view, *Syncerus caffer*

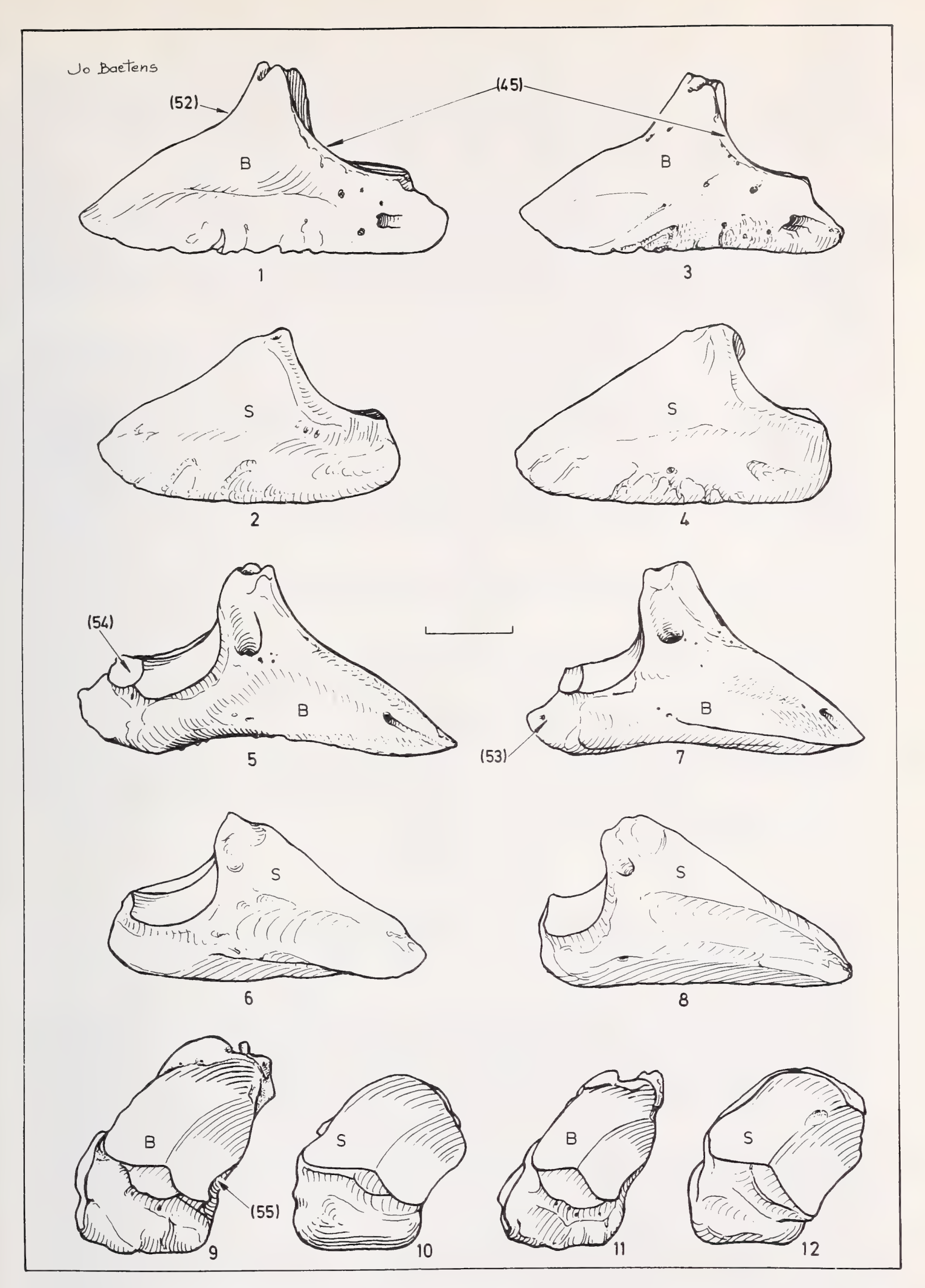


Plate 8. 1: P. distalis manus, abaxial view, *Bos primigenius* f. taurus, 2: P. distalis manus, abaxial view, *Syncerus caffer*, 3: P. distalis pedis, abaxial view, *Bos primigenius* f. taurus, 4: P. distalis pedis, abaxial view, *Syncerus caffer*, 5: P. distalis manus, axial view, *Bos primigenius* f. taurus, 6: P. distalis manus, axial view, *Syncerus caffer*, 7: P. distalis pedis, axial view, *Bos primigenius* f. taurus, 8: P. distalis pedis, axial view, *Syncerus caffer*, 9: P. distalis manus, proximal view, *Bos primigenius* f. taurus, 10: P. distalis manus, proximal view, *Syncerus caffer*, 11: P. distalis pedis, proximal view, *Bos primigenius* f. taurus, 12: P. distalis pedis, proximal view, *Syncerus caffer*

Ossa tarsi

Talus. In many cases, the caput tali exhibits in *Bos* at its facies articularis ossis centroquartalis a lateral groove, which is absent in *Syncerus* (pl. 5, figs. 1–2, char. 32).

Calcaneus. 1. In *Syncerus,* the sustentaculum tali is more pronounced medially (pl. 5, fig. 4) while in *Bos* it is more developed in a plantar direction (pl. 5, fig. 5, char. 33). 2. The proximal portion of the processus coracoideus is better developed dorsally in *Bos;* the transition towards the proximal part of the calcaneus lies more plantarly compared with *Syncerus* (pl. 5, fig. 5, char. 34).

Os centroquartale. 1. The plantar side of the lateral half of the os centroquartale exhibits in *Bos* a well pronounced plantar prominence, which is nearly absent in *Syncerus* (pl. 5, figs. 7–8, char. 35). 2. In *Bos,* the medioplantar portion of the proximal articular surface of the os centroquartale, which articulates with the caput tali, shows an extra articular surface laterally (pl. 5, figs. 9–10, char. 36). 3. The small, distal, lateroplantar articular surface, which articulates with a corresponding surface at the proximal extremity of the os metatarsale III + IV is in *Bos* generally smaller than in *Syncerus* (pl. 5, figs. 11–12, char. 37).

Os tarsale I. No constant osteomorphological differences were found.

Os tarsale II + III. No constant osteomorphological differences were found.

Os metatarsale III+IV

1. The habitus of the os metatarsale III+IV differs in the two genera: relatively slender in *Bos*, while shorter, broader and rather sturdy in *Syncerus* (pl. 5, figs. 17–18, char. 38).

2. The lateroplantar articular surface of the proximal epiphysis is much more developed laterally in *Syncerus* (pl. 5, figs. 15–16, char. 39).

Ossa digitorum

Criteria to distinguish the ossa digitorum manus from the ossa digitorum pedis in *Bos* and *Syncerus*

Phalanges proximales. 1. The habitus of the P. proximales pedis is more slender compared with that of the P. proximales manus (pl. 6, figs. 1–8, char. 40) (see also Dottrens, 1946:764). 2. The general appearance of the proximal end of the first phalanges is rather squarish for those of the fore limb and rather rectangular for those of the hind limb (pl. 6, figs. 9–16, char. 41) (see also Dottrens 1946:765). 3. In *Bos*, the articular surface for the axial os sesamoideum proximale of the P. proximales manus is reduced in size compared with that of the P. proximales pedis (pl. 6, figs. 9–16, char. 42) (see also Dottrens 1946:765).

Phalanges mediae. 1. The habitus of the P. mediae pedis of *Bos* and *Syncerus* is more slender compared with that of the P. mediae manus (pl. 7, figs. 1–8, char. 43) (see also Dottrens 1946:753). 2. The general appearance of the proximal end of the phalanges mediae is rather squarish for those of the fore limb, and rather rectangular for those of the hind limb (pl. 7, figs. 9–16, char. 44). 3. In *Bos*, the abaxiopalmar part of the trochlea phalangis mediae manus is more developed proximally compared with its analogue in the P. mediae pedis (pl. 7, figs. 5 and 7, char. 44a) (see also Dottrens, 1946:753).

Phalanges distales. In axial view, it becomes obvious that the margo coronalis of the distal phalanges of the hind limb exhibits a steeper course than that of the distal phalanges of the fore limb (pl. 8, figs. 5–8, char. 45) (see also DOTTRENS 1946:743).

Criteria to distinguish between the ossa digitorum from *Bos* and *Syncerus*

Phalanges proximales. 1. In both axial and abaxial view, one notices the angular aspect of the phalanges proximales in *Bos*, while in *Syncerus* these phalanges are more rounded (pl. 6, figs. 1–8, char. 46). We nevertheless agree with S. PAYNE (in litt.) that this criterium cannot always be used. 2. The proximal fovea articularis is well delineated in *Syncerus*, which is not the case in *Bos* (pl. 6, figs. 9–16, char. 47). 3. The facies articulares for the ossa sesamoidea proximalia are more pronounced in *Syncerus* compared with *Bos* (pl. 6, figs. 9–16, char. 48).

Phalanges mediae. 1. In *Syncerus*, the phalanges mediae generally show a more slender habitus compared with those from *Bos* (pl. 7, figs. 1–8, char. 49). 2. In *Syncerus*, the abaxiopalmar part of the trochlea phalangis mediae manus is less developed proximally compared with its analogue in *Bos* (pl. 7, figs. 5–6, char. 50). 3. The articular surface is divided into two glenoid cavities by a crista sagittalis. In *Bos*, the difference in size between the abaxial and axial glenoid cavities is much larger compared with *Syncerus* (pl. 7, figs. 9–16, char. 51). 4. In many cases, the abaxial tuberosity of the torus palmaris/plantaris is less pronounced in *Bos* (pl. 7, figs. 9–16, char. 51a) (see also PAYNE, unpublished report).

Phalanges distales. 1. The processus extensorius is more developed in *Bos* (pl. 8, figs. 1–8, char. 52). 2. The tuberculum flexorium is in *Bos* more pronounced in the palmar (P. distales manus) and plantar (P. distales pedis) direction (pl. 8, figs. 1–8, char. 53). 3. The facies articularis sesamoidea for the os sesamoideum distale is larger and lies more plantarly in *Bos* (pl. 8, figs. 9–12, char. 54). 4. In *Bos*, the axial border of the facies articularis is indented, which is not the case in *Syncerus* (pl. 8, figs. 9–12, char. 55).

Concluding remarks

From the foregoing, it should be clear that a number of diagnostic osteomorphological features exist which allow a distinction between African buffalo and cattle. Only a few smaller carpal and tarsal bones such as the os carpi accessorium, the os carpale IV, the os tarsale I and the os tarsale II+III cannot be separated yet morphologically. Due to the fact that many features are located near the articular surfaces of the bones, even incomplete bones – in casu fossil specimens – can now in many cases be identified to the species level.

During our analysis, we also found out that measurements, and the indices based on them, proved to be a less useful tool for the distinction between the skeletal elements of the two species, because of the large overlap.

We furthermore were able to check whether the osteomorphological characteristics, established for domestic cattle, were also applicable to its wild ancestor, the aurochs *(Bos primigenius)*. It is known that the domestication process causes morphological changes but, from our observations, we can conclude that most of the features of domestic cattle described above can also be used to identify its wild ancestor.

Acknowledgements

The author is indebted to Drs. A. GAUTIER, P. SIMOENS, Rijksuniversiteit Gent, and S. PAYNE, Cambridge University, for reading the manuscript and discussing the subject; to Drs. W. VAN NEER, Katholieke Universiteit Leuven, and J.-P. BRUGAL, C.N.R.S., Marseille, for their valuable comments;

to Drs. X. Misonne, Koninklijk Belgisch Instituut voor Natuurwetenschappen, Brussels, D. Thijs van den Audenaerde, D. Meirte, Koninklijk Museum voor Midden-Afrika, Tervuren, and J. Clutton-Brock and K. Bryan, British Museum Natural History, London, for the permission to study museum material; to J. Baetens for the drawings and to N. Reynaert for typing the manuscript. This study has been financed by the I.W.O.N.L., Brussels; a travel grant was provided by the Vlaamse Wetenschappelijke Stichting, Leuven.

Zusammenfassung

Osteomorphologische Unterscheidungsmerkmale am Gliedmaßenskelett vom afrikanischen Büffel (Syncerus caffer) und vom Hausrind (Bos primigenius f. taurus)

Knochenresten von diesen großen Boviden werden oft gefunden an afrikanischen holozänen archaeologischen Fundorten, aber ihre Bestimmung schafft manches Problem.

Ein Bestimmungsschlüssel wurde entwickelt, um dieses immer wiederkehrende Problem zu lösen; die diagnostischen, osteomorphologischen Merkmale, welche eine Unterscheidung beider Tierarten voneinander ermöglichen, werden festgelegt. Nur einige kleine Karpal- und Tarsalknochen können noch nicht unterschieden werden.

Im allgemeinen sind die osteomorphologischen Unterscheidungsmerkmale beständiger als die osteometrischen. Den größeren Teil dieser osteomorphologischen Charakteristiken, festgelegt für das Hausrind, kann man auch anwenden, um Knochenreste ihres Vorfahren, des Ur, zu bestimmen.

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Z. Säugetierkunde 53 (1988) 124–125

ISSN 0044-3468

WISSENSCHAFTLICHE KURZMITTEILUNGEN

Note on the skull size in the two sympatric Mouse Deer species, *Tragulus javanicus* (Osbeck, 1765) and *Tragulus napu* (F. Cuvier, 1822)

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Receipt of Ms. 15. 6. 1987

At present, within the family Tragulidae, the sister-group of the Cervidae, four species are recognized: viz. *Hyemoschus aquaticus* (Ogilby, 1841), living in tropical West Africa and Central Africa north of the Congo River; *Tragulus meminna* (Erxleben, 1777), occurring on Sri Lanka (Ceylon) and in the south of peninsular India, and the largely sympatric species *Tragulus javanicus* (Osbeck, 1765) and *Tragulus napu* (F. Cuvier, 1822), both found in southeast Asia and on islands west of the Strait of Makassar. The last two species strongly resemble each other. The only clear differences are found in their colour pattern, mainly of the throat area, and in size; *T. javanicus* being the smaller species and *T. napu* the larger one. Size differences are most distinct where the species live side by side, whereas in allopatric populations, *T. javanicus* can even be larger than *T. napu*.

When two species overlap geographically, the situation in which the differences between them are accentuated in the zone of sympatry, and weakened or lost entirely in parts of their ranges outside this zone is called: Character displacement; see Brown and Wilson 1956. *T. javanicus* and *T. napu* have been suggested (Dr. A. C. V. van Bemmel – in verbis) to be a nice example of this phenomenon, however without giving exact data.

During the first part of a study of the taxonomy and speciation of Tragulidae, over 200 skins and skulls of *T. javanicus* and *T. napu* have been studied, forming part of the collections of the Institute of Taxonomic Zoology (Zoological Museum) in Amsterdam, the Rijksmuseum van Natuurlijke Historie at Leiden and the British Museum (Natural History) in London. The author is grateful to the curators of the mentioned collections for the permission to study the material.

The differences in the dimensions of the skins of the two species were apparent and often documented by the measurements provided by the collectors. Nevertheless, to avoid possible mistakes caused by different ways of preparing the skins and taking the measurements, only the skull dimensions (taken by the author) were used. To simplify the graphic representation of the results, only the condylobasal lengths are given (see figure 1).

Comparing the condylobasal lengths of the skulls of allopatric populations with those of sympatric populations, it is obvious that character displacement in skull size is present in the two Mouse Deer species studied. It is necessary, however, to discuss also other influences which may have caused the observed differences. First the rule of Bergmann, which assumes that larger body size is selectively advantageous in colder climates. According to figure 1, this could be a possible explanation for the differences found in the more northern mainland populations and the more southern populations of Sumatra and Borneo of *T. napu*, were it not, that the differences in climate between the mentioned areas are slight. All the areas are within the region of tropical rain forests, although in the north

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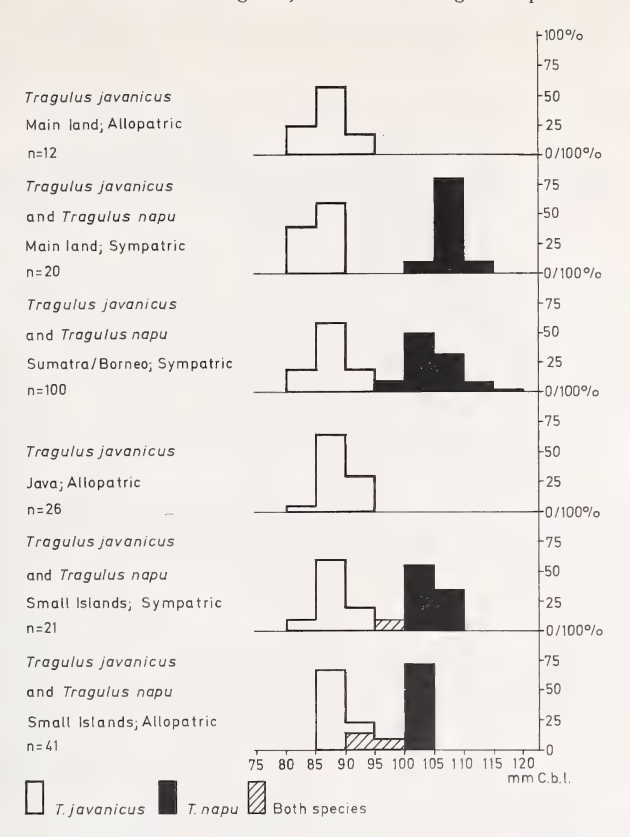


Fig. 1. Condylobasal lengths of 220 skulls of *Tragulus javanicus* and *Tragulus napu*, living allopatrically or sympatrically

somewhat more influenced by the different monsoons than in the south. Another phenomenon to be taken into account is that in mammals, representatives of species occurring on small islands sometimes tend to be smaller than members of the same species living on large islands and on the mainland. This phenomenon may play a role in *T. napu*, but not in *T. javanicus* (see figure 1). It can be ignored with regard to the differences observed between *Tragulus* species living on small islands, sympatrically or alone.

Summarizing, *Tragulus javanicus* and *Tragulus napu* show character displacement in skull size, when living sympatrically. They tend to reach more intermediate sizes when living without congeners.

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Z. Säugetierkunde 53 (1988) 126–127

ISSN 0044-3468

Deutsches Primatenzentrum, Göttingen

Nachtaktivität von Spitzhörnchen *(Tupaia belangeri)*

Von J. Kurre und E. Fuchs

Eingang des Ms. 23. 9. 1987

Zur Familie der Tupaiidae gehören mit Ausnahme von *Ptilocercus lowii* nur tagaktive Arten (Luckett 1980). Die Aktivität von *Tupaia glis* während der Hellphase erscheint u. a. darin begründet, daß ihre Retina nur aus Zapfen besteht (Samorajsky et al. 1966). Berichte über mögliche Nachtaktivitäten verschiedener *Tupaia*-Arten erscheinen teilweise widersprüchlich. Sprankel (1961) fand für *Tupaia glis*, daß Männchen nachts ohne Unterbrechung schlafen. Nachtaktivität beobachtete er nur bei hochträchtigen Weibchen; auch Inoué und Honda (1974) geben Nachtaktivität für weibliche *Tupaia glis* an. Sorenson und Conaway (1964, 1966) fanden bei Direktbeobachtungen für *T. longipes, T. gracilis, T. chinensis* und *T. tana* keine Nachtaktivität. Dagegen beschreiben Liu et al. (1982), ohne Angaben zur Methode zu machen, für *Tupaia belangeri (chinensis)* geringe Nachtaktivität.

Bei Untersuchungen individualtypischer Aktivitätsmuster von *Tupaia belangeri* stellten wir mit Passiv-Infrarotdetektoren (PID) fest, daß trotz völliger Dunkelheit in den Haltungsräumen einige Tiere nachts aktiv waren.

Beobachtet wurden insgesamt 16 adulte männliche Spitzhörnchen*(Tupaia belangeri)* aus dem Deutschen Primatenzentrum, Göttingen. Die Tiere lebten in vollklimatisierten Räumen einzeln in Edelstahlkäfigen, an deren Außenseite je ein hölzerner Nistkasten angebracht war. Zwischen benachbarten Käfigen befanden sich Sichtblenden. Die Lichtphase begann um 8.00 h und endete um 20.00 h. Futter (Tupaia-Standard-Diät, Altromin, Lage) und Wasser waren ad lib. vorhanden.

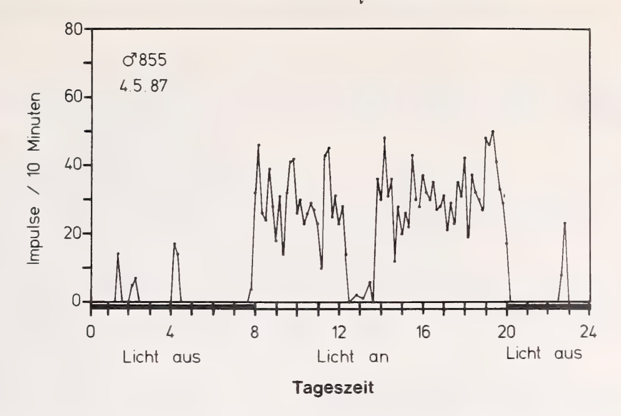
Die lokomotorische Aktivität wurde mit Passiv-Infrarot-Detektoren (PID) gemessen. Der Sensor dieses Systems (Superrot SR 2000 Passiv-Infrarot-Detektor, Visonic Ltd., Tel Aviv, Israel) bestand aus einem infrarotempfindlichen, pyroelektrischen Doppelelement, das gegen Luftströmungen und Änderungen der Umgebungstemperatur unempfindlich war. Es zeigte jedoch das Eindringen eines wärmeausstrahlenden Tieres in den vom Sensor abgetasteten Bereich an. Die Signale wurden als Summe in 10-Minuten-Intervallen von einem Epson Hand-Held HX 20-Computer registriert und auf einer Mikrokassette gespeichert. Von da wurden die Daten auf einen IBM-Personal Computer übertragen und mit „Lotus 1-2-3" (1983 Lotus Development Corporation) graphisch bearbeitet. Einzelheiten zur Methode s. Lerchl (1986).

Bei sechs von 16 untersuchten Tieren konnte mit der PID-Registrierung Nachtaktivität festgestellt werden. Die Tiere verließen in unregelmäßigen Abständen bis zu achtmal pro Nacht für bis zu 20 min ihren Nistkasten. Ein Beispiel (♂ 855) ist in Abb. 1 dargestellt.

Von zwei Tieren (♂ 855 und ♂ 1008) wurden mit Video je vier Nächte aufgezeichnet und ihre Nachtaktivitäten quantitativ und qualitativ untersucht. Wegen der völligen Dunkelheit in den Haltungsräumen beleuchteten wir die Käfige mit Infrarot-Lampen (Filter > 840 nm; Göttingen Farbfilter GmbH) und benutzten zur Aufzeichnung eine Infrarot-Kamera (Grundig SAE 70). Während der Nacht wurden die Tiere weder durch die Aufnahmen noch den Kassettenwechsel am Videorekorder gestört.

Beide untersuchten Tiere (♂ 855; ♂ 1008) waren nach Ende der Lichtphase noch bis zu 10 min aktiv (20.00–20.10 Uhr) bevor sie in ihre Nistkästen gingen. ♂ 1008 verließ seinen Nistkasten während der vier Nächte insgesamt dreimal für zwei bis sechs min, ♂ 855 insgesamt siebenmal für drei bis sechzehn min. An Bewegungsformen konnten nur Laufen und Klettern beobachtet werden. Das sonst für *T. belangeri* typische Springen trat in der Nacht nicht auf. Insgesamt waren die Bewegungen langsam und vorsichtig. Beim Laufen

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Motorische Aktivität von ♂ 855, registriert über 24 h. Die Hellphase dauerte von 8.00–20.00 Uhr

über Äste behielten die Tiere mit dem Bauch meist Kontakt zum Untergrund. Weiter wurden Fressen (max. 3:20 min), Trinken (max. sechsmal) und Körperpflege (max. 5:30 min) registriert. Vereinzelt konnten auch Markierverhalten sowie Koten beobachtet werden.

Unsere Beobachtungen zeigen, daß innerhalb der tagaktiven Arten der Tupaiidae, zumindest für *Tupaia belangeri,* Nachtaktivität generell nicht ausgeschlossen werden kann. Vergleicht man unsere Ergebnisse mit denen von Liu et al. (1982) und anderer Autoren, so scheint die Erfassung und Beschreibung von Nachtaktivität von den eingesetzten Beobachtungs- und Registriertechniken abhängig zu sein.

Danksagung

Herrn Prof. Dr. Erkert, Universität Tübingen, danken wir für die Überlassung der Infrarot-Kamera.

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Anschrift der Verfasser: Joachim Kurre und Dr. Eberhard Fuchs, Deutsches Primatenzentrum, Kellnerweg 4, D–3400 Göttingen

ZWEERS, G. A.; DULLEMEYER, P. (eds.): **Architecture in living structures.** Spec. publ. of Acta Biotheoretica Vol. 34. Boston, Lancester, Dordrecht: Nijhoff Publishers BV 1985. 184 pp. US $ 45.00. ISBN 90-247-3240-9

Die Veröffentlichung der 13 Beiträge zum 19. Lochmühle Symposion behandeln durchweg Fragen zur Methodik und Theorie einer Konstruktionsmorphologie (Funktionelle Morphologie i. S. der Leidener Arbeitsgruppe). Vorträge sehr verschiedenartig orientierter Forscher berichten über neue Ergebnisse unter funktionalen, strukturalistischen und transformistischen Aspekten und unter Heranziehen von Beispielen vorwiegend aus Forschungen an niederen Vertebraten (ein Beitrag handelt über Arthropoden). Der Begriff der Konstruktionsmorphologie geht auf den bedeutenden Entomologen HERMANN WEBER zurück, dessen grundlegende Arbeiten bisher leider in der Morphologie der Wirbeltiere meist übersehen wurden. Es ist dankbar zu begrüßen, daß durch den Beitrag von W. E. REIF, R. D. K. THOMAS und M. FISCHER mit Nachdruck auf das Werk WEBER's verwiesen wird, auch wenn dieses noch in die Zeit vor der allgemeinen Konzeption einer synthetischen Evolutionstheorie fällt und dadurch die Reserve WEBER's gegenüber einseitigen Überlegungen zur Evolutionsfrage verständlich werden. Der genannte Beitrag ist zugleich der einzige, der ein Beispiel aus der Morphologie der Säugetiere (Konstruktionsmorphologie und Stammesgeschichte der Hyracoidea durch M. FISCHER) einbezieht. Die Ausführungen von DULLEMEYER legen in klarer und weitgespannter Form die Problematik des Themas, die Methodik und wissenschaftstheoretische Einordnung dar. Gegenüber einigen stark reduktionistischen Auffassungen einiger Funktionalisten wird der integrative Charakter der modernen Konstruktionsmorphologie klargestellt und die Komplementarität verschiedener Betrachtungsweisen hervorgehoben.

D. STARCK, Frankfurt/M.

NACHTIGALL, W. (Hrsg.): **Bat flight – Fledermausflug.** BIONA report 5. Stuttgart, New York: Gustav Fischer Verlag 1986. XII, 235 S. Zahlreiche Abb. u. Tab. DM 38,–. ISBN 3-437-20372-X, ISSN 0930-0635

Der jetzt vorliegende fünfte BIONA-Report faßt – nach drei Bänden über den Vogel- und den Insektenflug und einem Werk über Thermobiologie – die Ergebnisse eines Symposiums zusammen, das im Mai 1984 in Saarbrücken unter der Leitung von WERNER NACHTIGALL stattfand. Themenschwerpunkt des Buches ist der Fledermausflug, doch sind in diesen Report auch Fragen der Flugbiophysik von Flugsauriern und Gleitbeutlern mit aufgenommen. Zusammen mit den bereits erschienenen Bänden 1–3 liegt damit jetzt eine Übersicht vor, die Probleme des Fluges aller wichtigen fliegenden Tiergruppen behandelt.

Acht Kapitel dieses Buches, jeweils den Sachgebieten „Evolution" und „Physiologie" zugeordnet, behandeln den Fledermausflug. Die Themen reichen von der reinen Biophysik, über Funktionsmorphologie und physiologische Energetik, bis hin zur mutmaßlichen Evolution des Chiropterenfluges. So wird die Evolution des Fluges (K. SCHOLEY) und die Entwicklung von Flug und Flügelformen (U. M. NORBERG) untersucht. Mechanik, Aerodynamik und Evolution des Fledermausfluges sind Thema eines weiteren Kapitels (J. RAYNER). Die Untersuchungen des Energiebudgets von blütenbesuchenden Fledermäusen zeigen, wie unermüdlich diese kleinen Tiere auf Nahrungssuche sein müssen, um überleben zu können (O. v. HELVERSEN). Die Korrelation von Flügelschlag und Lautaussendung wird in zwei weiteren Arbeiten beschrieben (K. HEBLICH, H. HERBERT).

Vier Artikel, unter dem Stichwort „Gleiter" zusammengefaßt, beschäftigen sich mit der Lokomotion des Taguan *(Petaurista petaurista)* (K. SCHOLEY) und einer allgemeinen Abhandlung über Flügelbaupläne (D. SCHALLER) sowie mit zwei typischen Bionik-Themen: So wird unter anderem anhand von Rauchkanalexperimenten aufgezeigt, daß Felloberflächen gegenüber glatten Flächen eine aerodynamisch günstige, grenzschichtstabilisierende Wirkung haben und die technische Nutzung dieser Erkenntnis diskutiert (W. NACHTIGALL). Als Randgebiet des Themenkreises ist schließlich die Beschreibung eines vor fast hundert Jahren gebauten Fledermausflugzeuges mit in diesem Band enthalten (B. KRESLING).

Das Buch, das neben den genannten Arbeiten von VON HELVERSEN, NACHTIGALL und NORBERG, Beiträge einer Reihe jüngerer Autoren enthält, wendet sich an Leser, die mit den Grundproblemen des (Fledermaus-) Fluges vertraut und an weiteren Einzelheiten zu diesem Thema interessiert sind.

EVELYN SCHLOSSER-STURM, Hamburg

Erscheinungsweise und Bezugspreis 1988: 6 Hefte bilden einen Band. Jahresabonnement Inland: 308,– DM zuzüglich 13,80 DM Versandkosten, Gesamtpreis 321,80 DM einschließlich 7 % Mehrwertsteuer. Jahresabonnement Ausland: 308,– DM zuzüglich 18,– DM Versandkosten. Das Abonnement wird zum Jahresanfang berechnet und zur Zahlung fällig. Es verlängert sich stillschweigend, wenn nicht spätestens am 15. November eine Abbestellung im Verlag vorliegt. Die Zeitschrift kann bei jeder Buchhandlung oder bei der Verlagsbuchhandlung Paul Parey, Spitalerstraße 12, D-2000 Hamburg 1, bestellt werden. Die Mitglieder der „Deutschen Gesellschaft für Säugetierkunde“ erhalten die Zeitschrift unberechnet im Rahmen des Mitgliedsbeitrages.

Z. Säugetierkunde 53 (1988) 2, 65–128

Vol. 53 (3), 129–192, Juni 1988 ISSN 0044-3468 C 21274 F

ZEITSCHRIFT FÜR SÄUGETIERKUNDE

INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Organ der Deutschen Gesellschaft für Säugetierkunde



Verlag Paul Parey Hamburg und Berlin

This journal is covered by Biosciences Information Service of Biological Abstracts, and by Current Contents (Series Agriculture, Biology, and Environmental Sciences) of Institute for Scientific Information

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Die Zeitschrift für Säugetierkunde veröffentlicht Originalarbeiten und wissenschaftliche Kurzmitteilungen aus dem Gesamtgebiet der Säugetierkunde, Besprechungen der wichtigsten internationalen Literatur sowie die Bekanntmachungen der Deutschen Gesellschaft für Säugetierkunde. Verantwortlicher Schriftleiter im Sinne des Hamburgischen Pressegesetzes ist Prof. Dr. Harald Schliemann.

Zusätzlich erscheint einmal im Jahr ein Heft mit den Abstracts der Vorträge, die auf der jeweiligen Hauptversammlung der Deutschen Gesellschaft für Säugetierkunde gehalten werden. Sie werden als Supplement dem betreffenden Jahrgang der Zeitschrift zugeordnet. Verantwortlich für ihren Inhalt sind ausschließlich die Autoren der Abstracts.

Manuskripte: Manuskriptsendungen sind zu richten an die Schriftleitung, z. Hd. Prof. Dr. Dieter Kruska, Institut für Haustierkunde, Biologie-Zentrum, Neue Universität, Olshausenstr. 40–60, D-2300 Kiel. Für die Publikation vorgesehene Manuskripte sollen gemäß den „Redaktionellen Richtlinien“ abgefaßt werden. In ihnen finden sich weitere Hinweise zur Annahme von Manuskripten, Bedingungen für die Veröffentlichung und die Drucklegung, ferner Richtlinien für die Abfassung eines Abstracts und eine Korrekturzeichentabelle. Die Richtlinien sind auf Anfrage bei der Schriftleitung und dem Verlag erhältlich.

Sonderdrucke: Anstelle einer Unkostenvergütung erhalten die Verfasser von Originalbeiträgen und Wissenschaftlichen Kurzmitteilungen 50 unberechnete Sonderdrucke. Mehrbedarf steht gegen Berechnung zur Verfügung, jedoch muß die Bestellung spätestens mit der Rücksendung der Korrekturfahnen erfolgen.

Mit zwei Beilagen des Verlages Paul Parey

Fortsetzung 3. Umschlagseite

Z. Säugetierkunde 53 (1988) 129–147

ISSN 0044-3468

Evolution and variation of antipredator vocalisations of Antelope squirrels, *Ammospermophilus* (Rodentia: Sciuridae)

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Receipt of Ms. 12. 01. 1987

Abstract

Analysis of variation in antipredator (alarm) vocalisations of North American antelope squirrels *(Ammospermophilus)* indicates the existence of significant differences among species, with little variation present among individuals, sexes, seasons and ambient temperature within species. Stepwise discriminant analysis of ten sonograph measurements for five species samples indicates that mean pulse duration, frequency of main sound energy, and frequency at beginning contribute most to species separation. The short harsh trill of *A. interpres, A. nelsoni,* and *A. insularis* appear to be adapted to closed habitats (rocky/prairie), and the long pure-toned trill of *A. harrisii* and *A. leucurus* to open desert conditions. Comparisons with the vocalisations of other sciurids suggest that the short calls are primitive, and that the evolution of long trills has accompanied the recent development of deserts in North America.

Introduction

There is widespread interest in the importance of vocalisations in the ecology and life-history of various groups of mammals (e.g., Kolb 1981; Rieger and Peters 1981; Schmidt et al. 1982; Peters 1982, 1984; Herbert 1983; Sieber 1985). Within the family Sciuridae vocalisations may constitute important factors in the evolution of sociality as they form the "glue" of their societies. Many descriptions and analyses of squirrel vocalisations examine aspects of variation within populations, and individual response to differing stimulus situations (see Owings and Hennessy 1984) but fewer attempt to assess variation among populations. Before the role of antipredator vocalisations (alarm calls) in sciurid ecology and evolution can be fully assessed it is desirable to understand more about the nature and levels of variation that exist within and among populations and species. This paper quantitatively analyses variation in antipredator vocalisations within and among the five living species of the genus *Ammospermophilus,* North American antelope squirrels, which have not been studied previously, and discusses the variation from ecological and evolutionary viewpoints.

Materials and methods

This study is based on vocalisation data from a total of 57 adult individuals representing the five *Ammospermophilus* species, *A. harrisii* (Har), *A. leucurus* (Leu), *A. insularis* (Ins), *A. interpres* (Int), *A. nelsoni* (Nel), and *Spermophilus variegatus* and *Sciurus niger* (see specimens examined).

In order to ensure that the samples measured included only adults, a survey was made to determine the condition of teeth and sutures in the skulls of individuals considered to be adults on the basis of their reproductive state (gravid or well-developed testes descended). All data are from adults by the criteria developed: fronto-parietal suture ankylosed (see also Callahan and Davis 1977) and the bregma completely closed (Hall 1926), yellow enamel on incisors, permanent upper P^3-M^3 present in occluding position (Hoffmeister and Diersing 1978; Robinson and Hoffmann 1975) except in *A. insularis,* which may lack P^3 and its alveolus. In addition, all skulls exhibited tooth wear (Beg and Hoffmann 1977; Callahan and Davis 1977).

All specimens were live-trapped and the vocalisations given in response to my presence immediately after capture were recorded on a UHER 4000L tape recorder (range 40–20000 cps) at 19.05 cm

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per s (7.5 ips), using a unidirectional microphone, with a level frequency response of 50–12000 cps, held approximately 40 cm from the subject. A total of 155 sonagrams were made in the frequency ranges 80–8000 Hz and 160–16000 Hz from the recordings with a Kay Sonograph 6061B using wide- and narrow-band filters, to emphasise time and frequency respectively. The frequency spectra of the calls is shown as a function of time; amplitude is proportional to blackness of the impression. Time was measured with the wide filter bandwidth, and frequency with narrow filter bandwidth.

Fifteen measurements were taken from the sonagraphs. Three highly correlated pairs of measurements were "redundant," and one of each was selected for further analysis. Two additional characters proved to be highly variable and also were eliminated. The following measurements taken from the sonagraphs were used in the analyses (DOC, DOT, MPD in s, the rest in kHz):
DOC – duration of call – length of call from first sound emitted to end of call;
DOT – duration of trill – length of trill from first clearly configured pulse to end of call;
MPD – mean pulse duration – the mean duration from the beginning of one pulse to the beginning of the next, measured at the beginning (from the third pulse), middle, and end of call;
FRO – frequency band around trill at onset of call, the range of frequencies emitted simultaneously in the noise characteristic of "kuk" (Horwich 1972);
FMT – frequency of main sound energy of the trill half way in its duration;
FBT – frequency of trill at beginning;
LFR – lowest frequency emitted;
FRF – frequency of the fundamental;
FRH – frequency of first harmonic above main sound energy;
CAR – cascade ratio, the ratio of the pitch at the beginning of the call to the pitch at one-half the length, where the amplitude is high.
Because some vertebrates exhibit variation in their vocalisations emitted at different temperatures, measurements were made to determine if vocal traits have any relationship to ambient temperature. The measured sonagrams for *A. nelsoni* and *A. leucurus* are from recordings made in the lab at 20 °C and 31 °C, with an hour difference in time. Data for *A. interpres* and *A. insularis* are from samples recorded at two ambient temperatures for each population in the field. *A. harrisii* was examined for variation at two different times of the year, during the reproductive season, November–May (descended testes, gravidity, lactation) and from the non-reproductive season, June–October.

Statistical analyses were carried out by use of BMDP programs (Dixon 1981). BMDP3D was used for univariate analyses including the comparisons of the variance of ten multiple calls of a single individual in each species with its respective species sample (50 F-tests) and for pair-wise comparisons among the five species (100 t-tests). These tests were applied also between all individuals of each sex in each species to estimate this possible source of variation. Stepwise discriminant function analysis was performed with BMDP7M, F-to-enter set at 4.0. For each of the first four vectors (variates) a standardised canonical coefficient, indicating the relative weight of each character for each variate, was computed by multiplying the canonical coefficient for the character by its pooled standard deviation. Cluster analyses were performed with BMDP2M, using Euclidean distance with unweighted variables and by cladistic analysis.

All specimens were prepared as standard skins, skulls, and postcranial skeletons to identify adults (of which vocalisations were measured), for future verification of species identities, and for adjunct studies of genetics and morphology, and ontogeny of vocalisations, and are deposited in the Natural History Museum of Los Angeles County: *Ammospermophilus leucurus,* 6 females, 4 males; *A. harrisii,* 13 females, 5 males; *A. nelsoni,* 11 females, 11 males; *A. interpres,* 3 females; *A. insularis,* two females, two males; *Spermophilus variegatus,* one male; *Sciurus niger,* one male. The small sample of four individuals of *A. insularis,* from a remote island, affects statistical analyses for similarity between species using the t-test, with greater likelihood of supporting the hypothesis of no difference. Also, the statistics methods take into account varying sample sizes.

Results

The alarm call vocalisation given by antelope squirrels (Fig. 1) is a trill as defined by Broughton (1963), a rapid succession of repeated sounds or "syllables," resolvable by the human ear, and has a narrow frequency envelope. The call may begin with a wide-frequency band of noise whose onset is sharp, and is followed immediately without a break in time by the more pure-toned trill. This initial rapid burst of sound, measured as the frequency around the trill at onset (FRO), is referred to here as "kuk," as it is similar in the structure of its wide range of frequencies to the "kuk" named and described by Horwich (1972) for *Sciurus carolinensis.*

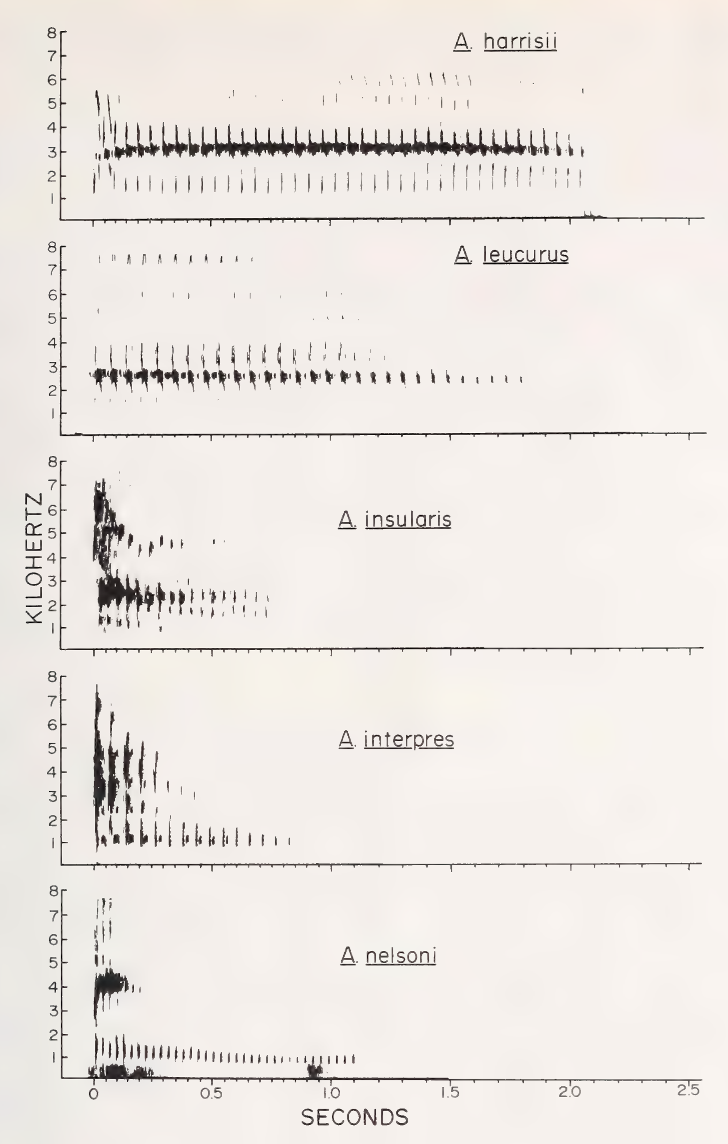


Fig. 1. Sonagrams of representative antipredator vocalisation of each of the five species of *Ammospermophilus*

Interspecific variation

Sonagraphs of calls from the five species of *Ammospermophilus* (Fig. 1) suggest that there are differences with respect to frequencies of main sound energy and fundamentals, harmonics and noise, length of call, and distance (time) between pulses of the trill. Also, the main sound energy may be the fundamental, or it may be an harmonic of the fundamental; there may be one or more harmonics above the main sound energy. *A. leucurus* and *A. harrisii* have calls that appear long, and relatively pure-toned, without a wide band of frequencies emitted at the beginning. *A. nelsoni, A. interpres,* and *A. insularis* appear to have a shorter call, with a wide band of frequencies at its onset. In addition, *A.*

interpres appears to have a longer pulse duration than any other species, *A. nelsoni* has a shorter pulse duration than any other species, and both have a noticeably deeper-pitched trill.

Univariate analysis of the data for ten alarm call measurements (Tab. 1) indicates significant differences (.05 confidence level) among the calls of the species (Tab. 2) ranging from one character (between *A. insularis* and *A. interpres*) to all ten (between *A. harrisii* and *A. nelsoni*). All the call characters differ between at least one species pair.

Duration of calls ($\overline{DOC}$ or mean DOC) is 2.13 s and 2.24 s in *A. leucurus* and *A. harrisii* respectively, and is approximately twice the length of the calls of *A. nelsoni* (1.05 s) and *A. interpres* (1.07 s), whereas *A. insularis* is intermediate (1.35 s). Duration of trill (DOT) is related to duration of call and varies from it by the duration of the kuk sound, if present. The kuk as measured by band of frequency at the beginning of the calls ($\overline{FRO}$) in *A. leucurus* and *A. harrisii* is small (2.48 and 2.22 kHz), but in the other species is broad, producing a sudden, loud harsh noise at the beginning of the call. Frequency of the main sound energy of the trill ($\overline{FMT}$), frequency of the first harmonic ($\overline{FRH}$), and frequency at the beginning of the trill ($\overline{FBT}$), are shared (i.e. not significantly different at .05 level) by *A. leucurus, A. harrisii* and *A. insularis,* the species with relatively high-pitched calls. These same three characters are shared by the two species with relatively low-pitched calls, *A. nelsoni* and *A. interpres.* The lowest frequency emitted ($\overline{LFR}$) and frequency of the fundamental ($\overline{FRF}$) are shared among all the species, except *A. nelsoni.* The mean pulse duration ($\overline{MPD}$) is shared by *A. leucurus* and *A. harrisii* ($\overline{MPD}$ = .052 and .050 s) and by *A. harrisii* and *A. insularis* ($\overline{MPD}$ = .044). In *A. interpes* this interval is longer ($\overline{MPD}$ = .063) and in *A. nelsoni,* half this length ($\overline{MPD}$ = .032).

Table 1. **Measurements of characters of alarm calls of 57 individuals of the five species of *Ammospermophilus***

Character Acronym	*A. nelsoni* N=22	*A interpres* N=3	*A. insularis* N=4	*A. leucurus* N=10	*A. harrisii* N=18
DOC	1.05 ± 0.09 0.37 – 2.34	1.07 ± 0.08 0.92 – 1.20	1.35 ± 0.34 0.82 – 2.28	2.13 ± 0.16 1.40 – 3.04	2.24 ± 0.15 1.30 – 3. 88
FRO	6.99 ± 0.34 1.00 – 7.80	6.43 ± 0.47 5.50 – 7.00	7.33 ± 0.17 7.00 – 7.80	2.48 ± 0.53 0.70 – 5.20	2.22 ± 0.38 0.60 – 6.50
MPD	.032 ± .001 .022 – .038	.063 ± .003 .060 – .070	.044 ± .001 .040 – .048	.052 ± .002 .047 – .062	.050 ± .001 .030 – .057
FMT	1.09 ± 0.05 0.70 – 1.80	1.90 ± 0.56 1.20 – 3.00	2.33 ± 0.43 1.20 – 3.30	2.50 ± 0.14 1.50 – 3.00	2.73 ± 0.10 1.80 – 3.20
CAR	1.30 ± 0.04 0.92 – 1.60	1.07 ± 0.07 1.00 – 1.20	1.00 ± 0.01 0.99 – 1.02	1.19 ± 0.08 1.00 – 1.87	1.01 ± 0.03 0.86 – 1.47
LFR	0.07 ± 0.04 0.00 – 0.50	0.57 ± 0.30 0.00 – 1.00	0.15 ± 0.09 0.00 – 0.30	1.21 ± 0.26 0.00 – 2.50	1.46 ± 0.18 0.00 – 2.60
FRF	1.05 ± 0.05 0.60 – 1.60	1.13 ± 0.19 0.90 – 1.50	1.00 ± 0.35 0.10 – 1.70	1.83 ± 0.21 1.10 – 2.90	2.03 ± 0.17 1.10 – 3.30
FBT	1.33 ± 0.05 1.00 – 2.17	2.00 ± 0.53 1.20 – 3.00	2.30 ± 0.41 1.20 – 3.22	2.89 ± 0.07 2.60 – 3.20	2.69 ± 0.09 1.80 – 3.30
FRH	2.70 ± 0.15 1.60 – 3.30	3.10 ± 0.85 2.20 – 4.80	4.50 ± 1.15 2.50 – 6.50	4.28 ± 0.31 3.70 – 5.30	4.62 ± 0.22 3.40 – 5.70
DOT	0.96 ± 0.08 0.37 – 1.60	1.07 ± 0.08 0.92 – 1.20	1.35 ± 0.34 0.82 – 2.28	2.13 ± 0.16 1.40 – 3.04	2.25 ± 0.16 1.30 – 3.88

Means ± standard errors shown over ranges. Character acronyms are explained in text; DOC, MPD, and DOT are time in seconds, others are frequencies in kilohertz

Table 2. **Matrix of alarm call characters in which *Ammospermophilus* species differ significantly ($\underline{P} \leq .05$), above diagonal, and those which they share ($\underline{P} > .05$), below diagonal**

	A. nelsoni	*A. interpres*	*A. insularis*	*A. leucurus*	*A. harrisii*
NEL		MPD, CAR, LFR, FBT, FMT	MDP, CAR, FBT, FMT, FRH	DOC, MDP, LFR, FRO, FRF, FBT, FMT, FRH, DOT	DOC, MPD, CAR, LFR, FRO, FRF, FBT, FMT, FRH, DOT
INT	DOC, FRO, FRF, FRH, DOT		MPD	DOC, MPD, FRO, FBT, DOT	DOC, MDP, FRO, FRF, FBT, FMT, FRH, DOT
INS	DOC, LFR, FRO, FRF, DOT	DOC, CAR, LFR, FRO, FRF, FBT, FMT, FRH, DOT		DOC, MPD, LFR, FRO, FBT, DOT	DOC, LFR, FRO, FRF, DOT
LEU	CAR	CAR, LFR, FRF, FMT, FRH	CAR, FRF, FMT, FRH		CAR
HAR	——	CAR, LFR	MPD, CAR, FBT, MFT, FRH	DOC, MPD, LFR, FRO, FRF, FBT, FMT, FRH, DOT	

Character acronyms explained in text

The cascade ratio (CAR) is the change in pitch from the beginning to the midpoint of the trill, where amplitude is high. These calls have a soft quiet end. This ratio of FBT/FMT is nearly 1.00 in calls that do not have a drop in pitch (*A. insularis, A. harrisii,* and *A. interpres*) and higher of course in calls that cascade: *A. nelsoni* has a mean cascade ratio of 1.30, and *A. leucurus,* $\overline{\text{CAR}}$ = 1.19.

To summarise, (Tab. 2) the alarm call characters that show the largest number of differences among the species of *Ammospermophilus* are mean pulse duration (MPD) (eight differences), frequency at beginning of trill (FBT) (seven differences), frequency band at onset (FRO), duration of call (DOC), and trill (DOT) (all with six differences). In duration of call (DOC) and frequency band at onset (FRO) *A. leucurus* and *A. harrisii* are similar, and distinguished from *A. nelsoni, A. interpres,* and *A. insularis* in which these characters are similar. In mean pulse duration (MPD) and frequency of main sound energy (FMT) *A. leucurus, A. harrisii* and *A. insularis* are the same, and differ from *A. nelsoni* and *A. interpres.*

Stepwise discriminant analysis of the ten sonagraph measurements for the five species of *Ammospermophilus* indicate significant separation between all five species centroids (Fig. 2). Eighty-nine percent of the total variation is explained by the first two canonical variates. Standardised coefficients for the first four canonical variates (Tab. 3) indicate that mean pulse duration (MPD) and frequency at beginning of the call (FBT) make the greatest contribution to the first canonical variate, MPD and frequency of the main sound energy, or pitch (FMT) to the second. Characters which never entered into the discriminant analysis were DOC, DOT, FRF, and LFR. FRH is not used in the analysis because it is not always present.

The first canonical variate separates *A. nelsoni* from all other samples, primarily by MPD and FBT. *A. interpres* is distinguished from all other species by the second canonical

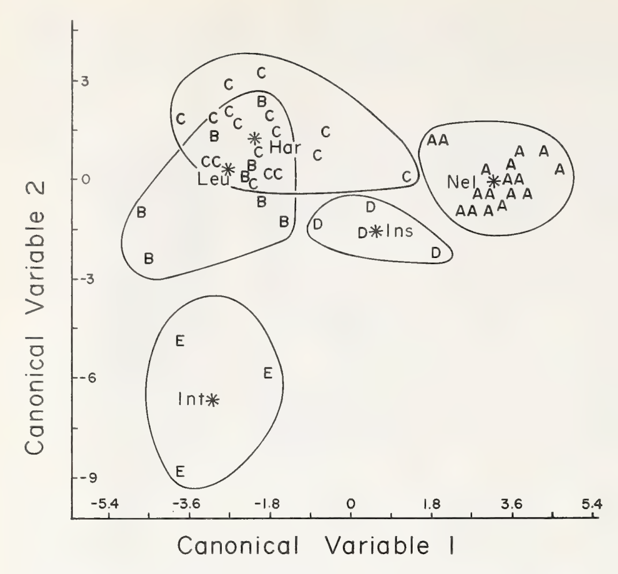


Fig. 2. Plot of the first two canonical variates, based on antipredator vocalisations, separating the five species of *Ammospermophilus*. Star indicates population centroids. The first variate (abscissa) represents 64 percent of the observed variance; the second (ordinate), 25 percent

variate, with MPD and FMT making the largest contribution. The distributions of individuals are separated for all species, except for *A. harrisii* and *A. leucurus*. The centroids for *A. leucurus* and *A. harrisii*, however, are significantly different ($D^2 = 16.16$, $\underline{P} = .005$). The separation of species by discriminant function analysis was mainly by mean pulse duration (MPD), and pitch (FMT and FBT).

An a posteriori classification (Tab. 4) correctly identified 90 % of the individuals. Three *A. leucurus* and two *A. harrisii* were cross-identified and one *A. harrisii* call was misassigned as *A. nelsoni*. All of the *A. nelsoni*, *A. insularis*, and *A. interpres* were correctly assigned. The percentage of

Table 3. **Standardized coefficients for canonical variates for the first four vectors for alarm calls of 57 individuals of five species of *Ammospermophilus***

	Canonical variates			
	1	2	3	4
Character				
MPD	−1.4687	−1.8912	−0.9294	0.9797
FRO	0.2981	−0.9237	0.0822	−0.5976
FMT	1.0515	1.6874	−4.3080	0.0300
FBT	−1.4209	−1.1105	3.8840	−0.5871
CAR	0.6544	0.8026	−1.7546	0.6013
% Variance explained	64.4	24.8	7.4	3.3

Table 4. **Classification matrix based on stepwise discriminant analysis of alarm calls of 57 individuals of the species of *Ammospermophilus***

Species	Percent Correct	Total	Number of cases classified into group NEL	LEU	HAR	INS	INT
A. nelsoni	100.0	22	22	0	0	0	0
A. leucurus	70.0	10	0	7	3	0	0
A. harrisii	83.3	18	1	2	15	0	0
A. insularis	100.0	4	0	0	0	4	0
A. interpres	100.0	3	0	0	0	0	3
Total	89.5	57	23	9	18	4	3

correct classification indicates the high degree of species specificity of alarm calls in *Ammospermophilus*.

The alarm vocalisations of the genus fall into two general types: harsh (wide band of frequencies at beginning), short, and with relatively low-pitched trill in *A. nelsoni*, *A. interpres* and *A. insularis;* and longer relatively pure-toned and higher-pitched trills in *A. leucurus* and *A. harrisii*. The greatest number of similarities (Table 2) are between *A. insularis* and *A. interpres*, and between *A. leucurus* and *A. harrisii*. *A. nelsoni* has five similarities each with *A. interpres* and *A. insularis*. *A. nelsoni* shares only one character with *A. leucurus*. *A. nelsoni* and *A. harrisii* differ in all ten characters. *A. leucurus* and *A. harrisii*, then, are similar, and *A. nelsoni*, *A. insularis*, and *A. interpres* have similar vocalisations. Cluster analysis (Fig. 3) based on Euclidean distance (d_{jk}) between the five distinct population suggests close phenetic relationship between *A. harrisii* and *A. leucurus*, with *A. nelsoni*, *A. interpres*, and *A. insularis* forming a second cluster.

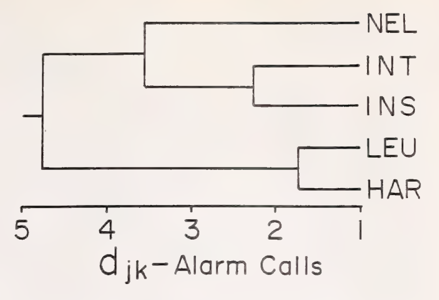


Fig. 3. Phenogram based on similarities of antipredator vocalisation characters in the five species of *Ammospermophilus*

Intraspecific and individual variation

For each of the five species, the variance for ten calls of an individual of each species was compared with the respective species sample. In each instance the within-individual variance (F-statistic, $\underline{P} \leq .05$) is significantly lower. This suggests that the species populations are separate taxa (species or subspecies).

There appears to be no sexual divocalism (sensu MARSHALL and MARSHALL 1976) in the structure of calls of *Ammospermophilus*. There are no significant differences ($\underline{P} \leq .05$) found between females and males in any character.

Individual *Ammospermophilus* do not show any differences ($\underline{P} \leq .05$) in four call characters examined (Tab. 5, DOC, MPD, FMT, FRO) at different ambient temperatures. No significant differences were found for the four characters between individuals of *A. harrisii* collected in the reproductive season and those from the non-reproductive season (Tab. 5).

Table 5. **Comparisons of means of characters of *Ammospermophilus* species calls recorded at (A) differing temperatures, and (B) differing times of year**

	A								B	
	A. nelsoni (KB 217)		*A. leucurus* (KB 232)		*A. interpres* (KB 167)		*A. insularis* (KB 119)		*A. harrisii*	
	n=1	n=3	n=3	n=3	n=3	n=3	n=3	n=3	n=9 Nov.-	n=9 June-
	20 °C	31 °C	20 °C	31 °C	24 °C	31 °C	24 °C	43 °C	May	October
Pitch (FMT)	1.30	1.13	2.73	2.73	1.30	1.17	1.13	1.16	2.73	2.71
Pulse rate (MPD)	.035	.034	.052	.051	.062	.061	.039	.039	.051	.048
Length of call (DOC)	1.45	1.21	1.57	1.57	1.01	0.93	1.11	1.38	2.47	2.02
"Kuk" frequency span (FRO)	6.70	6.73	4.23	3.43	4.93	6.80	7.30	7.10	2.11	2.33

Temperatures are in degrees Celsius; seasons of year explained in text; FMT, FRO in kilohertz, MDP, DOC in seconds. KB are field catalog numbers

Discussion

Interspecific variation

The vocalisations were recorded under similar circumstances and fulfill the criteria for homology of behaviors of TEMBROCK (1968): 1. the criterion of position (stimulus), 2. the criterion of special quality of structure (trill) and 3. the criterion of interconnection by intermediate forms (see transformation series discussed below). While an individual's antipredator call may exhibit large variation concomitant with varying stimuli (are not structurally unitary) (OWINGS and HENNESSY 1984) and dialects are described in squirrel subspecies (SLOBODCHIKOFF and COAST 1980), and these sources of variation may occur in *Ammospermophilus*, it is important that the conditions of collecting the sound recording be controlled for the kind of comparisons made in this study and which yield small intrapopulation variation. Thus these alarm calls of the five species of *Ammospermophilus* are homologues and possibly differ due to genetic differences between the species populations.

Although much work on birds suggest there is a large learning component in the forms of vocalisations (NOTTEBOHM 1972; KROODSMA 1982; KROODSMA and BAYLIS 1982; BAPTISTA and PETRINOVICH 1984) a genetic contribution may be larger in mammals. The most direct evidence for the inheritance of vocalisations in sciurids are the studies of interspecific hybrids in *Tamiasciurus* and *Spermophilus* that emit calls intermediate between those of the two parent species. Hybrid *Tamiasciurus hudsonicus* × *douglasii* emit three kinds of vocalisation, each intermediate in structure between those of the parents (SMITH 1978). *Spermophilus richardsonii* × *elegans* hybrids produce two types of vocalisations, the characters of which were consistent for each individual. The call characters of some hybrids are intermediate between parental species calls, and in others resemble one of the parent species (KOEPPL et al. 1978).

Ecological function of alarm calls

One source of the species specificity observed may be related to the functions of calls in different habitats. An important characteristic of alarm calls is the degree to which they may be located by the hearer. This function of a call may be achieved by its form (MARLER 1956; LEWIS and COLES 1983; LEWIS 1983). Broad band signals, whose sonagrams appear vertical, short, with much noise and subharmonics and a wide range of simultaneously emitted frequencies, tend to be easily located. The calls of *A. nelsoni, A. interpres,* and *A. insularis* are of this form, and both conspecifics and predators might determine more easily the location of the caller, and the predator.

Calls that result in pure-tone horizontal sonagrams are diffuse, and may be difficult to locate; this form is characteristic of calls of *A. leucurus* and *A. harrisii*. Thus the call types of *Ammospermophilus* may have important ecological consequences.

These two call types are associated with habitat types (Fig. 4). The association between physical aspects of the habitat and the structure of vocalisations is often observed (MARTIN and MARLER 1977; WILEY and RICHARDS 1978; PETERS 1984). The species that give the short, low-pitched call with broad frequency band at the beginning, *A. nelsoni, A. interpres,* and *A. insularis,* generally occur in more "closed" (non-open) habitats, rocky areas with dense vegetation (Fig. 5a–d), which occlude the view of a small ground squirrel. (They could also be interpreted as concealing habitats, or habitats with safe outlook perches.) *A. leucurus* and *A. harrisii* have a pure-toned call and occur in "open" sparsely vegetated xeric habitat (Fig. 5e, f). Interestingly, the association between habitat type and the length of call in the five *Ammospermophilus* populations contrasts with this trait and habitat in three populations of Gunnison's prairie dogs, *Cynomys gunnisoni* (SLOBODCHIKOFF and COAST 1980).

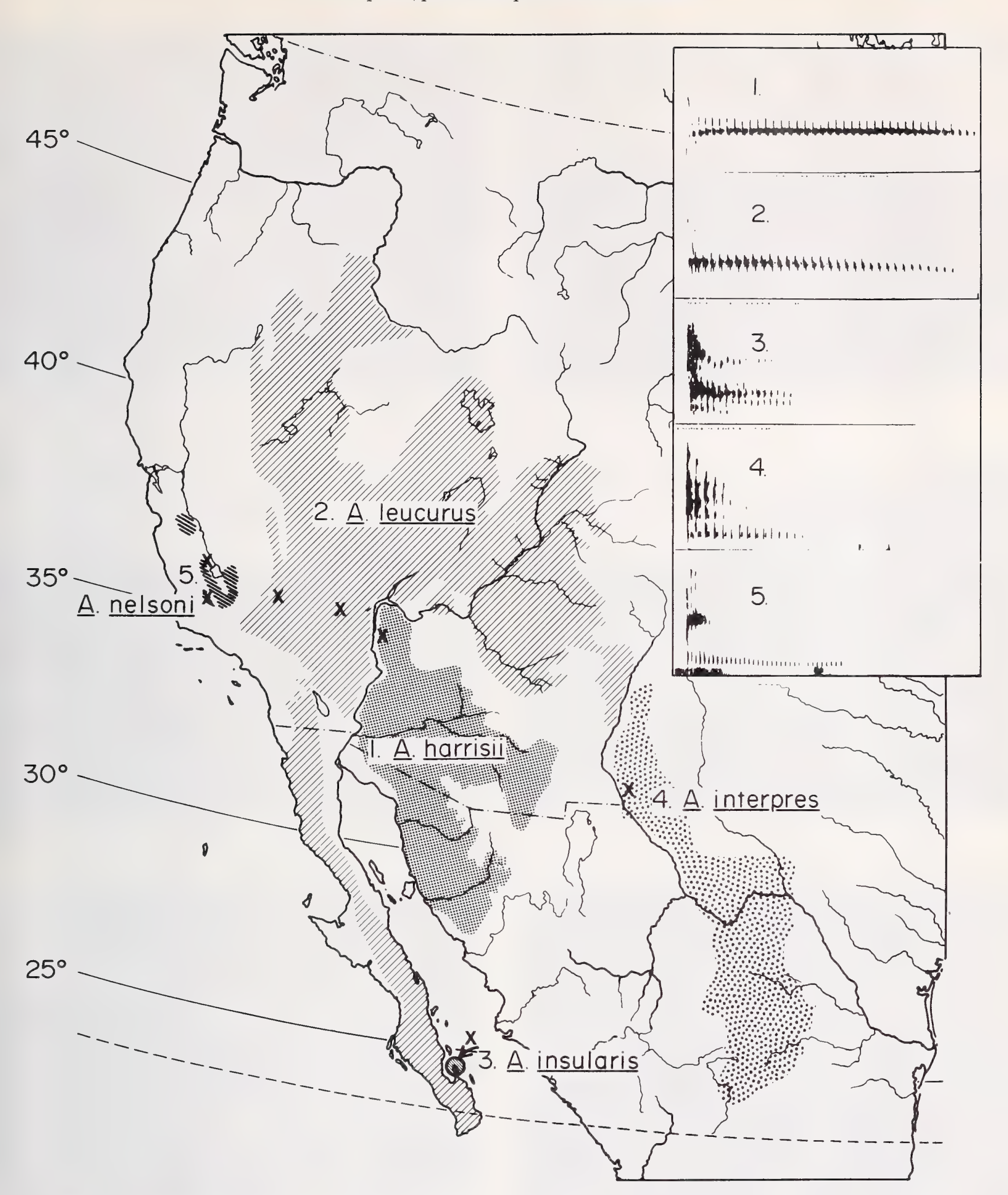


Fig. 4. Ranges in western United States and northern Mexico of the five extant species of *Ammospermophilus* with location of populations (X) from which vocalisations (insert) were analysed

The habitat of *A. nelsoni,* today and in the past (J. SAUER, pers. comm.) is primarily grassland, often tall enough to hide a small animal standing on the ground. Clearly, this habitat is, for the squirrel, a "closed" (non-open) habitat (Fig. 5a, b).

A. insularis occurs in highly rocky habitat with dense sub-tropical vegetation (Fig. 5d). It is abundant on rocky ridges and steep-walled canyons on Isla Espiritu Santo. The sarcocaulescent desert on the island approaches thornscrub in density, and contains many trees *(Cercidium, Bursera, Jatropha, Pachycereus)* (WIGGINS 1980).



Fig. 5. Habitats at localities from which the samples were collected for the five species of *Ammospermophilus*: A and B = *A. nelsoni*; C = *A. interpres*; D = *A. insularis*; E = *A. harrisii*; F = *A. leucurus*

A. interpres occurs in the Chihuahuan desert region, restricted to rocky foothills where it may be seen on tops of boulders, or in junipers. The species is generally absent from plains, plateaus and level, sandy terrain (FINDLEY et al. 1975) and prefers the rough, dissected cliffs and rocks at 1100–2000 meters elevation, often with woodland vegetation (SCHMIDLY 1977). The population studied was found at 1800 meters elevation on rocky mountain slopes covered by grassy, pinon-juniper woodland (Fig. 5c), a non-open habitat where individual squirrels are not readily visible.

The latter three species have a call with characteristics that suggest it is easily located. Possibly the calls relay awareness of the position of the predator to both conspecifics and the predator, while the squirrels have the relative security of concealment.

A. harrisii and *A. leucurus* inhabit the Sonoran, Mojave, and Great Basin Deserts. While *A. harrisii* occurs extensively in rocky areas with saguaro and paloverde vegetation, populations often live on sandy flats with relatively sparse treeless vegetation (*Larrea, Opuntia,* acaulescent yuccas) such as the habitat from which the study sample was collected (Fig. 5e).

Similarly, although *A. leucurus* inhabits a number of relatively closed habitats such as juniper-joshua tree woodland of the Mojave Desert, the species ranges extensively across open sandy treeless flats of *Artemesia, Larrea* or *Atriplex* in the Sonoran and Mojave Deserts, where the study sample was collected (Fig. 5f).

An individual *A. leucurus* or *A. harrisii* is usually visible when calling in a picket pin posture (GANDER 1967) from the ground, or from the top of a creosote bush (VAUGHAN 1954). To escape to a burrow it often must cover a wide expanse of open ground. The "tendency to run, rather than climb or seek nearby shelter, is reflected in the relatively longer feet of this species *[A. leucurus]* . . . in contrast to . . . *A. interpres,* which spends very little time away from rocks" (FINDLEY et al. 1975). Thus *A. leucurus* and *A. harrisii* sound an alarm that gives minimal information about their spacial position, while the three non-open habitat species can afford having a more informative, easily located call, which relays both position and alarm.

In addition to the above determinants of frequency band width (FRO) and call length (DOC), another trait concomitant with habitat is pitch of trill (FMT) for optimal transmission of sound. For maximum range of transmission, sounds produced within a few meters of the ground should be between one and four kHz in any habitat (WILEY and RICHARDS 1978).

These conclusions may explain the dominant mean frequency range of 1.09 to 2.73 kHz in alarm calls of *Ammospermophilus,* and suggest that transmission of their vocalisations may be optimal when they call from tops of large vegetation. While the differences in habitats for species of *Ammospermophilus* are considerably less than between tropical forest and grassland, trill pitch for four of the five species is consistent with the prediction of the MARTEN and MARLER (1977) model. *A. leucurus* and *A. harrisii* sampled from open desert have higher-pitched (2.50–2.73 kHz) calls. *A. nelsoni,* and *A. interpres* sampled from "non-open" habitat have calls with lower pitch (1.09–1.90 kHz). *A. insularis,* also from non-open habitat, does not fit this pattern for frequencies of main sound energy, with a mean pitch of 2.33 kHz.

Morphologic transformation

A transformation series is presented (Fig. 6) that hypothesises the sequence of evolutionary changes that may link the calls of *Ammospermophilus.* The calls of *A. interpres* (Fig. 6d, e, f, g) show greater variation in most characters of their alarm calls (similar to the structurally graded series of LEGER and OWINGS (1978) and OWINGS and HENNESSY (1984) than do other species of the genus. Individual calls of *A. interpres* are intermediate in form between calls of *A. harrisii* and *A. leucurus* which are at one end of the series, and the usual forms of *A. interpres, A. insularis* and *A. nelsoni* at the other end.

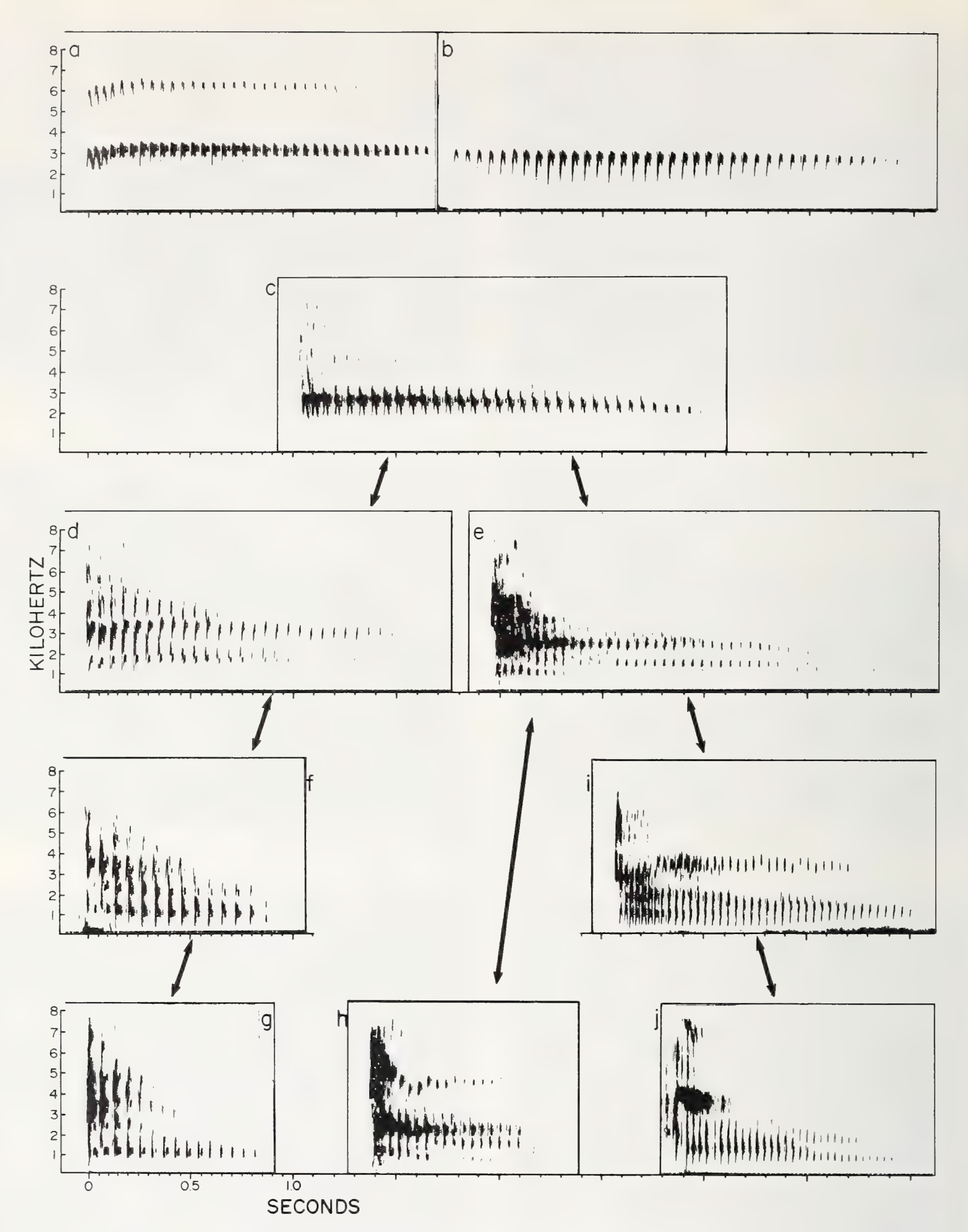


Fig. 6. Hypothetical transformation series for antipredator vocalisation structure in the five species of *Ammospermophilus*. Sonagrams are from a = *A. harrisii*; b and c = *A. leucurus*; d, e, f, and g = *A. interpres*; h and i = *A. insularis*; j = *A. nelsoni*

Sonagrams of calls of *A. interpres* that illustrate such intermediate variation form the basis of the transformation. From this morphoseries the sequence of evolutionary changes, but not its direction, can be inferred. The existence of such a series is also one of the criteria for homology (Tembrock 1968).

The calls of *A. harrisii* and *A. leucurus* (Fig. 6a, b, c) are high-pitched (FMT), long

(DOC), with wide pulse rate (MPD) and no "kuk" (FRO). At the other end of the spectrum are calls of *A. interpres* (Fig. 6g), *A. insularis* (Fig. 6h), and *A. nelsoni* (Fig. 6j) that are short with a broad band of frequencies at the onset, the "kuk" sound. One trend between the extremes is a shift in frequency of the trill by a change in emphasis to a fundamental (Fig. 6g and j) or an harmonic (Fig. 6g and j) emerging as fundamental (Fig. 6a and b). In general, there is gradation from the short pulse rate in short harsh calls (Fig. 6h and j) to the longer pulse rate of long pure-tone calls (Fig. 6a and b).

Although the gross appearance of the *A. insularis* call is similar to that of *A. interpres* and *A. nelsoni,* its pulse rate is longer (Fig. 6h). The pulse rate of *A. insularis* is not statistically different ($\underline{P} \leq .05$) from those of *A. leucurus* and *A. harrisii* (Fig. 6a, b, c). The pitch also does not change (statistically) in this morphoseries from *A. insularis* to *A. leucurus-A. harrisii.* The range of variation in these characters suggests that *A. insularis, A. leucurus,* and *A. harrisii* are not different in MPD. Also, *A. insularis,* and *A. interpres* may be transitional between *A. nelsoni* and *A. leucurus-A. harrisii.*

Phylogeny based on antipredator vocalisations

The utility of behavior as a taxonomic tool for the establishment of phylogenetic relationships among rodents has been largely neglected, although species-specific calls have been described for a number of groups (e.g. Clark 1974; Greene 1978; Greene and Burghardt 1978; Koeppl et al. 1978; Matocha 1975; Nikolskii 1974, 1976, 1979; Smith 1978), and evolutionary interpretations based on other behaviors have appeared for other vertebrates (e.g., Collias and Collias 1977; Marshall and Marshall 1976; McCarley and McCarley 1976; Struhsaker 1970).

To utilize the call transformation series to estimate phylogenetic relationships and derived characters it is rooted by outgroup comparison. Although many specific behaviors could be compared for this purpose, vocalisations are ideal because they may be visually and quantitatively represented on the sound spectrogram. Also, alarm calls are one of the communication behaviors of squirrels which are important in their social structure and evolution (Sherman 1977).

Trills similar to those of *Ammospermophilus* occur in a few other sciurids. Those which resemble them are often preceded by a sound, whose onset is sudden and com-

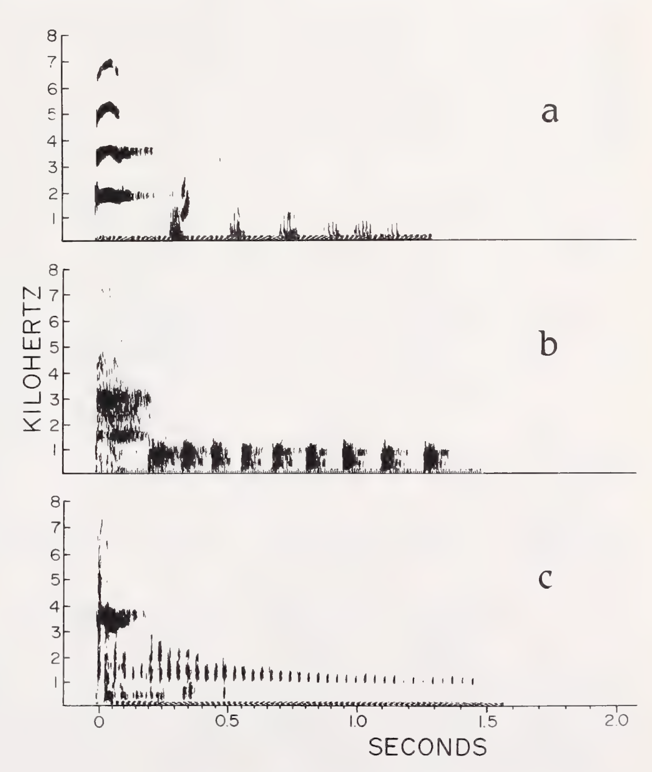


Fig. 7. Sonagrams of antipredator vocalisations of a = *Spermophilus variegatus*, b = *Sciurus niger*, c = *Ammospermophilus nelsoni*

posed of a wide band of simultaneously emitted frequencies. These are emitted by chipmunks, *Eutamias* (Brand 1976; Callahan 1980; Dunford and Davis 1975), grey squirrels, *Sciurus carolinensis* (Horwich 1972) and fox squirrels, *Sciurus niger* (Zelley 1971). I recorded similar vocalisations (Fig. 7) given by *Sciurus niger* (fox squirrel) and *Spermophilus (Otospermophilus) variegatus* (a rock squirrel) that appear to be homologous to *Ammospermophilus* vocalisations by the criteria of Tembrock (1968). These sounds were recorded and used to represent an out-group, termed "Sciuridae" (Fig. 8). *Sciurus niger* and *Spermophilus (Otospermophilus) variegatus* are anatomically relatively generalised members of the family Sciuridae (Black 1963; Long and Captain 1974; Wilson 1960) and as such constitute a reasonable outgroup for analysis of *Ammospermophilus,* for whom the sister group is unknown. Antipredator alarm trills occur in other ground squirrels in the holarctic subgenus *Spermophilus (Spermophilus)* which also inhabit new xeric habitats (Balph and Balph 1966; Melchior 1971; Betts 1976; Leger et al. 1984). They also are present in the subgenus *Spermophilus (Ictidomys)* (Harris 1967; Schwagmeyer and Brown 1981). However, the trills of these species are dissimilar to those of *Ammospermophilus* in having longer pulse rates, higher pitch and no "kuk." If the vocalisations of these taxa are used as an outgroup, the "kuk" element is left unanalysed.

Five measurements from sonagrams of the calls of these squirrels (Tab. 6) are compared by use of cladistic methods (Hennig 1979). These measurements are the salient varying characters in *Ammospermophilus.* The cladogram (Fig. 8) is rooted in the alarm calls of "Sciuridae" consisting of a "kuk" and a pure-toned, pulsed "buzz" (Horwich 1972) or trill.

It is difficult to determine whether quantitative characteristics are shared or different when mean values for all the taxa form a continuum. I estimated the confidence limits of all means by use of two standard errors averaged for the three large samples to determine overlap between samples. This method minimizes the effects of the disparate sample sizes. This approach is employed to determine relative primitive and derived character states. A multiple state transformation series (Hennig 1979; Bretsky 1979) is assumed to exist. Each significantly different ($\underline{P} \leq .05$) mean is considered to represent a character state. Relative derived states, (Tab. 6, Fig. 8) are indicated by succeedingly larger number of superscripts and are based on the assumption that evolution is parsimoniously unidirectional.

All *Ammospermophilus* differ from "Sciuridae" in having a significantly more rapid pulse rate, the trill (MPD, e′-e‴), and higher pitch (FMT, c′-c‴). Character states e′ and c′ are synapomorphies (shared derived characters) of the genus. *A. nelsoni* shares no additional derived characters within *Ammospermophilus* and thus occupies the first branch within the genus. This species possesses an autapomorphy (unique derived character state) in MPD (e‴). The remaining four species share a derived, higher-pitched call (FMT, c″-c‴). *A. insularis, A. leucurus,* and *A. harrisii* possess a derived higher frequency harmonic (FRH, d′). *A. leucurus* and *A. harrisii* are terminal sister taxa united by a highly derived long (DOC, a′), and pure-toned (FRO, b″, or loss of "kuk") vocalisation. These two species differ from one another only in their cascade ratio (CAR). There are only two homoplasies (convergence/reversal) in the tree: e″ in *A. nelsoni* and b′ in *A. interpres.*

History of antipredator vocalisations of *Ammospermophilus*

Comparisons with the vocalisations of other sciurids suggest that the short harsh calls of the geographically disjunct *A. insularis, A. interpres,* and *A. nelsoni* are primitive and that the long pure-toned trills of *A. leucurus* and *A. harrisii* are derived.

Because the changes inferred in vocalisation characteristics within the genus may have occurred facilely and rapidly, the shared derived similarities between *A. leucurus* and *A. harrisii* could be interpreted as having been 1. independently derived, or 2. inherited

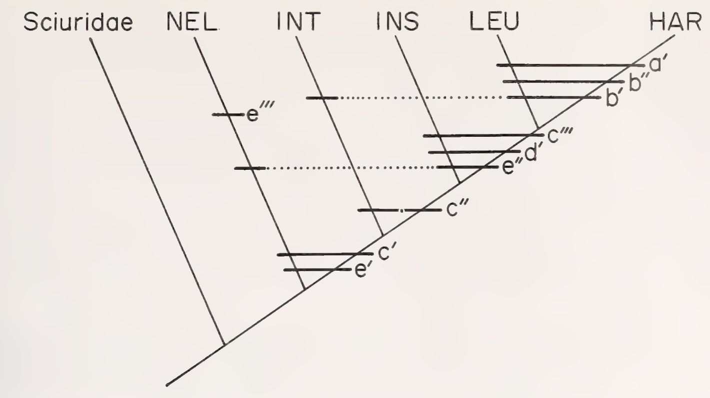


Fig. 8. Cladogram based on multiple state transformation series of antipredator vocalisations of the five species of *Ammospermophilus: A. nelsoni* (NEL), *A. interpres* (INT), *A. insularis* (INS), *A. leucurus* (LEU), and *A. harrisii* (HAR), using *Spermophilus variegatus* and *Sciurus niger* as the outgroup "Sciuridae". Letters code character states as in Table 6

from a common ancestor which formerly occurred throughout their combined ranges. However, analysis of skull morphology (Bolles unpubl.) support the latter hypothesis; *A. leucurus* and *A. harrisii* are phenetically most similar to one another and are probably each other's closest relatives.

Ecological considerations suggest that *A. insularis, A. interpres,* and *A. nelsoni* are adapted to closed habitats and *A. leucurus* and *A. harrisii* to open desert conditions. These conclusions are consistent with what is known of the late Tertiary and Pleistocene history of the southwestern United States and northern Mexico. Thorn forest occurred through the late Tertiary (Axelrod 1979) over much of what is today the Sonoran Desert, whereas the Mojave and most of the Great Basin were dominated by oak-pinon woodland (Axelrod 1979) until recent times.

Table 6. **Mean values of characters of alarm calls of *Ammospermophilus* and two other sciurid species**

	Duration of Call (DOC) Seconds		"kuk" Frequency Span (FRO) Kilohertz		Pitch (FMT) Kilohertz		Frequency of Harmonic (FRH) Kilohertz		Pulse Rate (MPD) Seconds	
Sciurus niger N = 4	1.41	a	7.62	b	.73	c	2.77	d	0.133	e
Spermophilus variegatus N = 7	1.27	a	7.47	b	.51	c	—	d	1.600	e
Ammospermophilus nelsoni N = 22	1.05	a	6.99	b	1.09	c'	2.17	d	0.032	e'''
Ammospermophilus interpres N = 3	1.07	a	6.43	b'	1.90	c''	3.10	d	0.063	e'
Ammospermophilus insularis N = 4	1.35	a	7.33	b	2.33	c'''	4.50	d'	0.044	e''
Ammospermophilus leucurus N = 10	2.13	a'	2.48	b''	2.50	c'''	4.28	d'	0.052	e''
Ammospermophilus harrisii N = 18	2.24	a'	2.22	b''	2.73	c'''	4.62	d'	0.050	e''

Late Wisconsin floras of the entire Southwest (from 22–17 thousand to 12–11 thousand ybp) (radiocarbon years before present) were pinon-juniper at mid-elevations (1525–5500 m) (Martin and Mehringer 1965; Van Devender et al. 1977; Raven and Axelrod 1978; Van Devender and Spaulding 1979). The McKittrick tar pits which contain *A. nelsoni* (Schultz 1938) have a flora that indicates a relatively closed pinon-juniper woodland and chapparal *(Pinus, Juniperus, Atriplex, Arctostaphylos)* (Mason 1944). Packrat middens collected in the Mojave Desert dated at 10000 ybp contain predominantly pinon-juniper woodland species: *Pinus, Juniperus, Fraxinus* and *Arctostaphylos* (Wells and Berger 1967). The entrance of the present dominant species of all North American deserts, creosote *(Larrea divaricata),* has been documented at less than 10000 ybp (Johnson 1976; Wells and Hunziker 1976).

During full glaciations of the Pleistocene, desert floras were restricted to a narrow zone in the lower Colorado River valley and Gulf of California coast north of the tropic scrub (Martin and Mehringer 1965). Floristic changes 8000–4000 ybp suggest an Altitermal (Xerothermic) climate (Axelrod 1966, 1979) during which desert species now separated by higher-elevation oak-pinon-juniper forest such as *A. leucurus* and *A. nelsoni* may have had continuous distributions (Munz 1974). There may have been continuous non-open habitat for populations of *Ammospermophilus* as late as 10000 ybp. Although the occurrence of the open-adapted *A. harrisii* and *A. leucurus* between the ranges of *A. interpres, A. nelsoni* and *A. insularis* could date from earlier times, the former two species may have originated with the expanding post-Wisconsin deserts. As recently as 4000 ybp, *A. leucurus* and *A. nelsoni* may have been in contact across the southern Sierra Nevada and Transverse ranges. The alarm vocalisation of *A. leucurus* and *A. harrisii* must be of very recent origin as are other behavioral, physiological, and anatomical adaptations for survival in an extremely xeric habitat (Bartholomew and Hudson 1959; Hudson 1962; Kavanau and Rischer 1972; Maxson and Morton 1974).

Acknowledgements

I thank N. E. Collias for his advice and for use of his laboratory facilities for the study of vocalisations; I am grateful also to R. L. Bezy, W. J. Dixon, R. Goldberg, C. Jacobs, M. Greenfield, and E. C. Olson for their interest and advice during this study, and especially grateful to Robert L. Bezy for his participation in the field. H. Walter generously provided the Abstract in German. L. Smith did the word processing. Permission to collect *Ammospermophilus* was kindly extended by Dr. Landazuri Ortiz, Direccion General de la Fauna Silvestre de Mexico, and by the State of California Department of Fish and Game, Arizona Game and Fish Commission, and New Mexico Department of Fish and Game. Financial assistance was provided by three research and field grants from the University of California Regents, and Office of Academic Computing.

Zusammenfassung

Zur Evolution und Variation der Warnrufe der nordamerikanischen Zieselgattung Ammospermophilus (Rodentia: Sciuridae)

Eine Analyse der Variation der Warnrufe nordamerikanischer Ziesel der Gattung *Ammospermophilus* zeigt, daß signifikante Unterschiede zwischen den Arten bestehen, während innerhalb einer Art nur geringe Unterschiede zwischen Individuen, Geschlecht, Jahreszeit und Umwelttemperaturen bestehen. Das Ergebnis der Diskriminanzanalyse von zehn Lautparametern legt nahe, daß das durchschnittliche Zeitintervall zwischen Lautelementen, die Schallfrequenz des energiereichsten Rufsegments und die des Rufanfangs am meisten zur Artentrennung beitragen. Der kurze und rauhe Triller von *A. interpres, A. nelsoni* und *A. insularis* scheint an Felsen- und Präriebiotope angepaßt zu sein, der lange und reine Triller von *A. harrisii* und *A. leucurus* dagegen an offene Wüstenbiotope.

Vergleiche mit den Alarmrufen anderer Hörnchen lassen den Schluß zu, daß die kurzen Rufe primitiv sind und die Evolution der langen Triller eine Folgeerscheinung der rezenten Ausbreitung von Wüstenbiotopen in Nordamerika ist.

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Z. Säugetierkunde 53 (1988) 148–161

ISSN 0044-3468

Robertsonian karyotype variation in the European house mouse, *Mus musculus*

Survey of present knowledge and new observations

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Receipt of Ms. 26. 1. 1987

Abstract

The karyotype of the European long-tailed house mouse, *Mus musculus,* was studied from Zadar (Yugoslavia) and Ammoudia (Greece). In mice from Zadar six and in those from Ammoudia three Robertsonian (Rb) chromosomes were present and have been identified by their G-band pattern. The composition of some of these marker chromosomes was unknown before, whereas some have been found to occur in other, geographically separated populations. The karyological details of both populations of the East-European distribution area were discussed together with observations on the karyotype of mice from Central and Western Europe and from Northern Africa.

Fertility data of a feral mouse from Zadar, which was heterozygous for one Rb chromosome, show that this particular genotype does not necessarily imply impairment of fertility in wild mice, which is mainly present in Rb heterozygous animals with a mixed genetic background of wild and laboratory mice. The Rb heterozygosity dependent impairment of fertility is due to segregational disorders during meiosis I.

Introduction

Evans et al. (1967) and Leonard and Decknudt (1967) were first to report the occurrence of a metacentric chromosome in laboratory mouse strains, and more findings of the same kind became known thereafter (see Gropp and Winking 1981). Similar changes, though with multiple pairs of metacentric chromosomes, were detected shortly later in wild mice from the Poschiavo valley in Southern Switzerland (Gropp et al. 1970), as well as from other areas of the Rhaetian Alps (Gropp et al. 1972). It became clear that these observations correspond to chromosome rearrangements in a complex system of balanced Robertsonian (Rb) variation, i.e. to changes due to centric translocations of two acrocentric chromosomes and commensurate reduction of the total number of chromosomes (Matthey 1966). The before mentioned and subsequent reports (Capanna et al. 1976; v. Lehmann and Radbruch 1977; Dulić et al. 1980; Adolph and Klein 1981, 1983; Gropp et al. 1982; Said et al. 1986) dealt with the occurrence, composition and characteristics of Rb metacentric chromosomes in mice obtained from local populations in the central (Lombardy, Switzerland, Germany), southern (Appennines, Sicily), or western (Spain, Scotland) Europe and North Africa (Tunesia). Only little information exists, however, about the karyotype patterns of house mouse populations from eastern and southeastern Europe. It appeared worthwile to supplement the so far scarce cytogenetic data about this region by new and recent observations on mice from Yugoslavia and Greece, and to collect available, though scattered, karyogeographic data for an update comprehensive survey of the occurrence and distribution of Rb chromosome variability in the house mouse, including the derived laboratory strains.

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Material and methods

Sixteen mice were trapped on two occasions near Zadar (Dalmatia), namely 10 animals in 1978 and six animals in 1981. A second site of investigation, about 640 kms southeast on the Adriatico-Ionian coast-line, is Ammoudia (Epiros: Northeastern Greece) from where 19 mice were analysed in 1980.

Karyotypes were established on lymphocyte metaphases from short time cultures (Triman et al. 1975) of peripheral blood cells. The blood samples were obtained by puncture of the retro-orbital sinus taken either from the original wild trapped mice (Zadar) or from their F-1 offspring with DBA/2 females (Greece). The identification of individual chromosomes was made on G-banded metaphases (Seabright 1971) using the criteria of the standard mouse karyotype presented by Nesbitt and Franke (1973). The designation of the Rb metacentric chromosomes and the arm composition followed the rules of the Committee on Standardized Nomenclature for Mice (1979). In addition, fertility of one natural male hybrid (Zadar) and of laboratory bred males derived from an interpopulation cross (Zadar × Poschiavo, see Table 4) was assessed by evaluation of matings with normal fertile laboratory female mice and by testis histology.

Results

Chromosome findings in mice from Zadar (Dalmatia)

The cytogenetic findings, in particular the observation of Rb metacentric chromosomes and their arm composition, are recorded in Table 1. 15 among the 16 animals showed a homozygous karyotype with six pairs of metacentric chromosomes and seven pairs of acrocentric autosomes plus the sex chromosome pair (Fig. 1). The remaining individual, which belonged to the 1978 sample, exhibited homozygosity for five pairs of Rb metacentrics only, and heterozygosity for the Rb(8.17)38Lub metacentric, corresponding to a karyotype with an odd number of 11 metacentrics, 16 acrocentrics and the sex chromosomes.

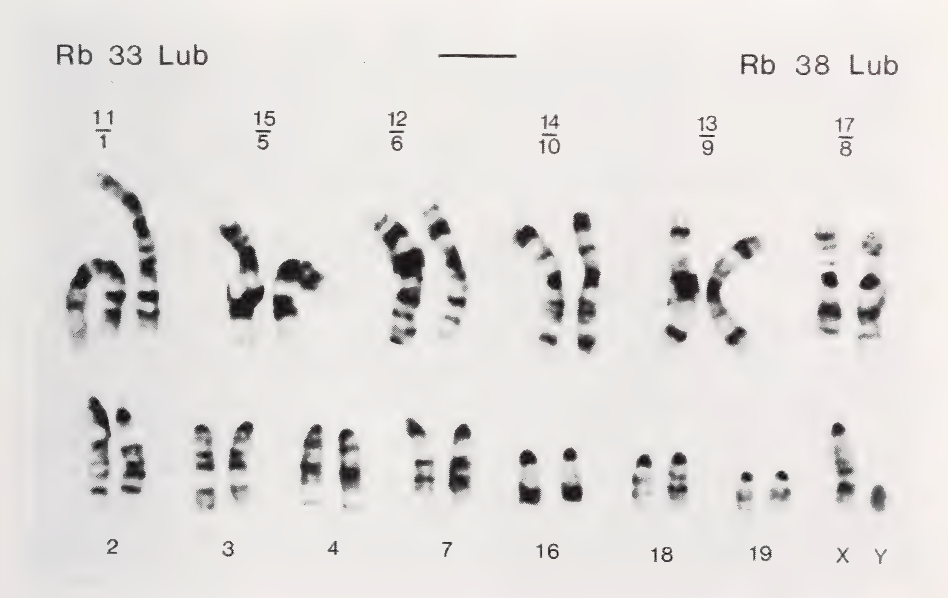


Fig. 1. G-banded karyotype of a male mouse from Zadar (Yougoslavia) with six pairs of Rb chromosomes. Numbers refer to chromosomes of the standard karyotype of the mouse

Chromosome findings in mice from Ammoudia (Greece)

The karyotype of 19 wild trapped males was established by studying their 34 offspring from crosses with DBA/2 females. In conventional chromosome preparations obtained from the F-1 progeny of 19 feral males, none, one or two Rb translocation metacentrics were found. However, from G-banding analyses it could be inferred that three different Rb translocations with a 3.10, 5.12 and 15.17 composition are present in this population (Table 2). The cytogenetic findings in the analysed progeny of the 19 wild trapped males are summarized in Table 2. From the mode of transmission of the Rb metacentric chromosome into the F-1 descendants, it can be concluded that eight of the original males must have been heterozygous for one or more Rb translocations. Interestingly heterozygosity for all three Rb chromosomes of the investigated population must have occurred in at least one of the original males. This indicates that the Ammoudia mouse population is very heterogeneous. It seems possible that a few more Rb metacentric chromosomes are present in the small sample investigated, but were not transmitted to the limited number of karyotyped F-1 offspring.

Table 1. **Arm composition and designation of Rb translocations of mice trapped near Zadar (Yougoslavia) and Ammoudia (Greece)**

Rb translocations found in mice from Zadar[1]	Ammoudia[2]
Rb (1.11) 33 Lub	Rb (15.17) 64 Lub
Rb (5.15) 34 Lub	Rb (3.10) 65 Lub
Rb (6.12) 35 Lub	Rb (5.12) 66 Lub
Rb (10.14) 36 Lub	
Rb (9.13) 37 Lub	
Rb (8.17) 38 Lub	

[1] Populations highly homogeneous for Rb translocations: 15 among 16 animals were homozygous for all of the six Rb chromosomes (see text). – [2] Population highly heterogeneous for Rb translocations (see Table 2 and text)

Table 2. **Karyotype of first or second offspring of wild males (Ammoudia) with DBA/2 females**

Current no of wild males	Karyotypes of first	or	second progeny
1	acrocentrics only		Rb (3.10) 65 Lub/+
2	acrocentrics only		Rb (3.10) 65 Lub/+
3	Rb (3.10) 65 Lub/+		Rb (3.10) 65 Lub/+
4	Rb (3.10) 65 Lub/+		Rb (3.10) 65 Lub/+
5	acrocentrics only		acrocentrics only
6	acrocentrics only		Rb (15.17) 64 Lub/+
7	acrocentrics only		Rb (15.17) 64 Lub/+
8	acrocentrics only		–
9	Rb (3.10) 65 Lub/+		Rb (3.10) 65 Lub/+ and Rb (5.12) 66 Lub
10	acrocentrics only		–
11	Rb (5.12) 66 Lub/+ and (Rb (15.17) 64 Lub		Rb (15.17) 64 Lub/+
12	Rb (3.10) 65 Lub/+		Rb (3.10) 65 Lub/+
13	acrocentrics only		Rb (15.17) 64 Lub/+
14	Rb (3.10) 65 Lub/+		Rb (3.10) 65 Lub/+
15	acrocentrics only		acrocentrics only
16	acrocentrics only		Rb (3.10) 65 Lub/+
17	acrocentrics only		acrocentrics only
18	Rb (3.10) 65 Lub/+		–
19	Rb (3.10) 65 Lub/+		–

Karyogeographic evaluation of the findings in Zadar and Ammoudia

Three of the Rb metacentric chromosomes found in Zadar (Dalmatia), i.e. (6.12), (10.14) and (8.17), show an arm composition identical to Rb chromosomes found in a mouse

population near Palermo (v. LEHMANN and RADBRUCH 1977), and two of them, (10.14) and (8.17), were shown to occur in mice from southern Germany (ADOLPH and KLEIN 1981). The Rb metacentric chromosome with the (5.15) arm composition occurs in a wide geographical range between Zadar (Dalmatia), central and northern Italy, Switzerland (CAPANNA et al. 1976; GROPP et al. 1982) and Spain (ADOLPH and KLEIN 1981). Hence, the geographical distribution of this particular Rb metacentric chromosome follows an eastwestward direction. The (1.11) chromosome is likewise present in the northern African population (Monastir, Tunesia: SAID et al. 1986), but the (9.13) chromosome of the Zadar population as well as two of the three Rb chromosomes of the Ammoudia (Greece) mice, i.e. (3.10) and (5.12) are unique among the Robertsonian chromosomes so far known from feral mouse populations (GROPP and WINKING 1981; BROOKER 1982; ADOLPH and KLEIN 1981; 1983).

Fertility of the natural hybrid found in Zadar

Heterozygosity of metacentrics of feral origin within a laboratory mouse genome may cause meiotic anaphase I nondisjunction. This leads to the formation of unbalanced gametes which transmit the aneuploid genome into the zygote. As a consequence the litter size is reduced at a commensurate rate, since whole arm aneuploidies are subject to selective elimination during pregnancy (CATTANACH and MOSELEY 1973; GROPP et al. 1974). While such segregational disorders are mainly known from heterozygotes for Rb translocations introduced from feral mice into laboratory strains, no comparable knowledge exists about Rb heterozygosity in a natural population. Therefore, the Zadar male with Rb(8.17)38Lub heterozygosity was mated several times with all acrocentric outbred NMRI females. The pregnant mothers were sacrificed at day 13 of pregnancy (plug day = day 1) and the numbers of corpora lutea and implants were recorded. Chromosome preparations were made from the fetal membranes of all alive implants. For comparison breeding records were established from males with the same Rb chromosome after introduction by five consecutive backcrosses into a laboratory mouse genome (NMRI) and from other Rb(8.17) heterozygous males, whose 8.17 Rb chromosome had a different source. One of these is the Rb(8.17)1Iem chromosome detected by BARANOV and DYBAN (1971) in a laboratory strain, and a second one is the Rb(8.17)6Sic chromosome isolated from a wild mouse of a Sicilian population with a series of seven metacentrics (v. LEHMANN and RADBRUCH 1977). This latter chromosome has been isolated and is now carried on a mixed background of wild and laboratory derived genes. The results of the breeding experiments as shown in Table 3 provide no evidence for the existence of noteworthy

Table 3. **Effect of heterozygosity in males for Rb (8.17) translocations of different origin upon fertility[1]**

Rb chromosome	no of pregnant ♀♀	no of corpora lutea	no of implants	percentage of resorptions	percentage of euploid implants	percentage of aneuploid implants
Rb (8.17) 38 Lub/+ natural hybrid	7	86	80	1.3	98.7	–
Rb (8.17) 38 Lub/+ laboratory mouse genome	14	177	152	38.8	61.2	–
Rb (8.17) 6 Sic/+ laboratory mouse genome	10	139	121	19.8	79.3	0.9[2]
Rb (8.17) 1 Iem/+ laboratory mouse genome	10	144	126	9.5	90.5	–

[1] Data refer to observations on fetal progeny at day 13 sired by heterozygous fathers and all acrocentric mothers (NMRI). – [2] One embryo with 39 chromosome arms; presumably X0

disturbances of meiotic segregation in the Rb(8.17)38Lub/+ natural hybrid male, since the day 13 fetal progeny contains only a very low rate of resorptions. In addition there is no evidence for an increased rate of preimplantation losses. While the respective proportions of preimplantation losses are in the same low range in the progeny of both other Rb(8.17) heterozygotes, these show higher postimplantation losses than the Rb38Lub heterozygous feral male. Surprisingly the highest postimplantation losses, however, were found in crosses with Rb(8.17)38Lub/+ males, which carried the Rb chromosome in a laboratory mouse genome. The correspondence of the respective proportions of aneuploid MII plates in Rb1Iem/+, Rb6Sic/+ and Rb38Lub/+ males with a laboratory mouse genome to the resorption rates lead us to assume that a major part of the resorptions is caused by chromosomal imbalance of the fetuses. In the Rb38Lub/+ feral male, even though MII evaluations were not possible, since the only available male died prior to the end of the breeding experiments, a correspondence of meiotic malsegregation rates and postimplantation losses has to be postulated.

Cytogenetic and reproductive analysis of laboratory hybrids bred from "Zadar" with multimetacentric type mice of different origin

Breeding assays of animals with newly identified Rb translocations against mice with a set of already known Rb chromosomes bear two advantages. Firstly, the type of pairing figures observed in 1st meiotic prophase can be used for examination on the correctness of the arm assignments of Rb translocations. Secondly, it provides information about the influence of complex Rb heterozygosity upon fertility. Both aims were borne in mind when males of the Zadar colony were crossed with females with the Rb1Bnr-7Bnr chromosome set ("tobacco mouse" – poschiavinus type). In case of proper identification of the "Zadar" metacentric chromosomes (see Tab. 1), the six "Zadar" and the seven "poschiavinus" metacentrics should be arranged in meiotic prophase of the hybrids in two chains of six and of five Rb metacentrics plus one ring bivalent of metacentric chromosomes. In fact, such pattern was observed in diakinesis figures. The male hybrids with such chains were sterile, and in the testis a severe manifestation of spermatogenetic arrest was observed in histological sections suggesting a breakdown of spermiogenesis during meiosis or shortly thereafter. This finding supports observations reported by Searle et al. (1978), Evans (1976) and Gropp et al. (1982) that chain formation during prophase of meiosis I has a harmful effect upon the process of spermatogenesis.

Discussion

Survey of a present knowledge about Robertsonian variation in laboratory and wild caught mice

By means of biochemical and morphological characteristics two groups within the species *Mus musculus* can be recognized in Europe (Zimmermann 1949; Thaler et al. 1981).

Geographically one group consisting of the three subspecies "*domesticus, brevirostris* and *praetextus*" occupies areas west of a line running from the Baltic sea through Germany and down to the Black sea. The second group taxonomically designed as *M. m. musculus* is distributed east to the beforementioned borderline (see: Orsini et al. 1983 and Fig. 2). Besides *M. musculus,* at least, two further *Mus* species exist in Europe occurring sympatrically with one or the other of the *M. musculus* subspecies, namely *M. spretus* in southwestern Europe and one *Mus* species in southeastern Europe, which is known as *Mus* 4 (Thaler et al. 1981). A common karyological denominator to all these species are acrocentric chromosomes, and an all acrocentric karyotype can be considered as the



Fig. 2. Geographical sites of house mouse populations with Rb chromosomes in Western Europe and Northern Africa. Characteristics of each population are given in Tab. 4. Solid line represents borderline of the western and eastern subspecies of *M. musculus* (see: ORSINI et al. 1983)

standard karyotype of the longtailed house mouse, *M. musculus*, as well as of the Asiatic subspecies of the house mouse.

The presence of Robertsonian translocations is a special trait of the *domesticus, brevirostris, praetextus* group of *M. musculus*. Moreover, this karyotypic variability seems to be limited to the European and African distribution area of house mice of this group. Altogether 22 different and characteristic Rb-constitutions have been found in the western part of Europe and Africa. The locations and the combinations of Rb-chromosomes present are listed in Fig. 2 and Table 4. Although *"domesticus/brevirostris"* type mice invaded large areas outside Europe along the routes of world traffic, at least few reports exist on the presence of Robertsonian translocations in natural populations like in Marion Island (ROBINSON 1978) far outside of Europe. In addition, two further reports about the occurrence of Robertsonian translocations in Asiatic house mice exist in the literature (CHAKRABARTI and CHAKRABARTI 1977; MORIWAKI et al. 1984). On the other hand, spontaneous Rb variation is known to occur in laboratory mice, whose biochemical and mitochondrial DNA characteristics have been shown to belong mainly to a *"domesticus"* background (YONEKAWA et al. 1980; FERRIS et al. 1982). Altogether 22 different Rb metacentrics have been described in laboratory stocks (see: GROPP and WINKING 1981; SEARLE and BEECHEY 1986). In contrast to wild mice all autosomes are involved in laboratory-type Rb translocations. In additoin, one case of an X-chromosome translocation onto autosome 3 (ARROYO NOMBELA and RODRIGUEZ MURCIA 1977) has been described. In contrast, a Robertsonian Y-autosome translocation has never been observed.

Table 4. **Arm composition, designation and derivation of Rb-chromosomes in feral mouse populations of Europe and northern Africa**

Arm composition/ designation	Locality	No of locality (see Fig. 2)	References
Rb (1.11) 33 Lub	Zadar	1	this paper
Rb (5.15) 34 Lub			
Rb (6.12) 35 Lub			
Rb (10.14) 36 Lub			
Rb (9.13) 37 Lub			
Rb (8.17) 38 Lub			
Rb (15.17) 64 Lub	Ammoudia	2	this paper
Rb (3.10) 65 Lub			
Rb (5.12) 66 Lub			
Rb (3.4) 1 Sic	Palermo	3	v. Lehmann and Radbruch 1977
Rb (2.15) 2 Sic			
Rb (6.12) 3 Sic			
Rb (5.13) 4 Sic			
Rb (10.14) 5 Sic			
Rb (8.17) 6 Sic			
Rb (9.16) 7 Sic			
Rb (1.2) 18 Lub	Island of Lipari	4	Gropp and Winking 1981
Rb (4.13) 19 Lub			
Rb (3.9) 20 Lub			
Rb (5.14) 21 Lub			
Rb (8.12) 22 Lub			
Rb (10.15) 23 Lub			
Rb (6.16) 24 Lub			
Rb (1.18) 10 Rma	Campobasso	5	Capanna et al. 1976
Rb (2.17) 11 Rma			
Rb (4.11) 12 Rma			
Rb (6.7) 13 Rma			
Rb (3.13) 14 Rma			
Rb (5.15) 15 Rma			
Rb (8.14) 16 Rma			
Rb (10.12) 17 Rma			
Rb (9.16) 18 Rma			
Rb (1.7) 1 Rma	Cittaduccale	6	Capanna et al. 1976
Rb (3.8) 2 Rma			
Rb (6.13) 3 Rma			
Rb (4.15) 4 Rma			
Rb (10.11) 5 Rma			
Rb (2.18) 6 Rma			
Rb (5.17) 7 Rma			
Rb (12.14) 8 Rma			
Rb (9.16) 9 Rma			
Rb (1.2) 10 Lub	Ancarano	7	Gropp and Winking 1981
Rb (5.13) 11 Lub			
Rb (3.9) 12 Lub			
Rb (4.17) 13 Lub			
Rb (6.16) 14 Lub			
Rb (8.14) 15 Lub			
Rb (10.12) 16 Lub			
Rb (11.15) 17 Lub			
Rb (2.4) 25 Lub	several places near Milano	8	Gropp et al. 1982
Rb (3.6) 26 Lub			
Rb (5.15) 27 Lub			
Rb (7.8) 28 Lub			
Rb (10.12) 29 Lub			
Rb (11.13) 30 Lub			
Rb (9.14) 31 Lub			
Rb (16.17) 32 Lub			
Rb (3.4) 39 Lub	Gallarate	9	Winking and Gropp 1983
Rb (2.8) 40 Lub			
Rb (6.7) 41 Lub			
Rb (5.15) 42 Lub			
Rb (10.12) 43 Lub			
Rb (11.13) 44 Lub			
Rb (9.14) 45 Lub			
Rb (16.17) 46 Lub			
Rb (1.6) 47 Lub	Cremona	10	Gropp and Winking 1981
Rb (3.4) 48 Lub			
Rb (2.8) 49 Lub			
Rb (5.15) 50 Lub			
Rb (10.12) 51 Lub			
Rb (11.13) 52 Lub			
Rb (9.14) 53 Lub			
Rb (16.17) 54 Lub			
Rb (7.18) 55 Lub			
Rb (1.3) 1 Lub	Bergamo, Ardenno, Sondrio	11	Gropp et al. 1982
Rb (2.8) 2 Lub			
Rb (4.6) 3 Lub			
Rb (5.15) 4 Lub			
Rb (10.12) 5 Lub			
Rb (11.13) 6 Lub			
Rb (9.14) 7 Lub			
Rb (16.17) 8 Lub			
Rb (7.18) 9 Lub			
Rb (1.3) 56 Lub	Sondalo	12	Gropp et al. 1982
Rb (2.8) 57 Lub			
Rb (4.6) 58 Lub			
Rb (5.15) 59 Lub			
Rb (10.12) 60 Lub			
Rb (11.13) 61 Lub			
Rb (9.14) 62 Lub			
Rb (16.17) 63 Lub			
Rb (1.3) 1 Bnr	Brusio, Sondalo	13	Gropp et al. 1970; 1982
Rb (4.6) 2 Bnr			
Rb (5.15) 3 Bnr			
Rb (11.13) 4 Bnr			
Rb (8.12) 5 Bnr			
Rb (9.14) 6 Bnr			
Rb (16.17) 7 Bnr			

Table 4 (continued)

Arm composition/ designation	Locality	No of locality (see Fig. 2)	References
Rb (10.11) 8 Bnr Rb (4.12) 9 Bnr Rb (1.10) 10 Bnr Rb (2.14) 11 Bnr Rb (7.8) 12 Bnr Rb (13.16) 13 Bnr	several Alpine valleys, Bondo, Roveredo, Chiavenna	14	Gropp et al. 1972
Rb (2.4) 67 Lub Rb (3.8) 68 Lub Rb (6.7) 69 Lub Rb (5.13) 70 Lub Rb (10.12) 71 Lub Rb (9.14) 72 Lub Rb (11.18) 73 Lub Rb (16.17) 74 Lub	Luino, Northern, Italy	15	Gropp et al. 1982
Rb (4.12) 1 Tu Rb (2.15) 2 Tu Rb (3.6) 3 Tu Rb (8.17) 4 Tu Rb (10.14) 5 Tu Rb (11.13) 6 Tu Rb (5.15) 16 Tu Rb (13.14) 17 Tu Rb (5.14) 18 Tu Rb (1.5) 19 Tu Rb (3.8) 20 Tu Rb (6.10) 21 Tu Rb (7.18) 22 Tu Rb (8.10) 23 Tu Rb (9.14) 24 Tu Rb (10.14) 25 Tu Rb (11.16) 26 Tu	several places in Southern Germany	16	Adolph and Klein 1981; 1983
Rb (4.12) 1 Nam	Belgium	17	Hübner 1985
Rb (3.14) 7 Tu Rb (4.10) 8 Tu Rb (9.12) 10 Tu Rb (6.14)	Orkney islands	18	Adolph and Klein 1981; Brooker 1982
Rb (4.10) 8 Tu Rb (6.13) 9 Tu Rb (9.12) 10 Tu Rb (11.17) Rb (10.14) Rb (4.8) Rb (1.11) Rb (8.17) Rb (8.14) Rb (15.17) Rb (3.8) Rb (8.15) Rb (3.16) Rb (17.18) Rb (11.14)	Castle-town, Caithness	19	Adolph and Klein 1981; Brooker 1982
Rb (4.14) 11 Tu Rb (5.15) 12 Tu Rb (6.10) 13 Tu Rb (9.11) 14 Tu Rb (12.13) 15 Tu	places near Barcelona	20	Adolph and Klein 1981
Rb (13.16) 1 Mpl	Ibiza	21	Britton-Davidian 1983
Rb (1.11) 2 Mpl Rb (2.16) 3 Mpl Rb (3.12) 4 Mpl Rb (4.6) 5 Mpl Rb (5.14) 6 Mpl Rb (7.18) 7 Mpl Rb (8.9) 8 Mpl Rb (10.17) 9 Mpl Rb (13.15) 10 Mpl	Monastir	22	Said et al. 1986

Some Rb chromosomes with similar arm composition as those observed in laboratory stocks were found in natural house mouse populations demonstrating that translocation events independently can occur involving the same chromosomes. Another point of interest is that some Rb's of laboratory mice have been found in strains already containing a metacentric derived from a feral mouse (Gropp and Winking 1981). This leads to the conclusion that the introduction of preexisting Rb metacentric chromosomes into the laboratory genome is not essential for the occurrence of Robertsonian changes in laboratory strain. However, it may facilitate or enhance the generation of this type of chromosomal rearrangement.

Considerably higher numbers of Rb translocation chromosomes have been found in populations of wild living house mice. Together with the three Rb metacentrics from Dalmatia and Greece described in this report the total number of Rb chromosomes with

different arm composition amounts to 77. A list of update completeness recording all so far described Rb chromosomes using the current designation according to the arm composition and the nomenclature rules (see: GROPP and WINKING 1981) is shown in Table 5. 42 Rb metacentrics were observed in only one population or geographic site, whereas 35 Rb chromosomes were found at least twice and up to ten times with a mean occurrence of 2.1.

Table 5. **Composition and frequency of Rb translocations in karyotypically distinct populations of feral mice. Rb translocations of laboratory origin are marked by an asterisk**

Composition	Frequency	Composition	Frequency	Composition	Frequency	Composition	Frequency
1.2	2	3.10	1	6.10	2	10.11	2
1.2*	1	3.12	1	6.12	2	10.12	8
1.3	3	3.13	1	6.13	2	10.14	5
1.5	1	3.14	1	6.13*	1	10.14*	1
1.6	1	3.15*	1	6.14	1	10.15	1
1.7	1	3.16	1	6.15*	1	10.17	1
1.10	1	3.X*	1	6.16	2	11.13	7
1.11	3	4.6	4	6.19*	1	11.14	1
1.15*	1	4.8	1	7.8	2	11.14*	1
1.18	1	4.10	2	7.13*	1	11.15	1
2.3*	1	4.11	1	7.18	4	11.16	1
2.4	2	4.12	3	8.9	1	11.16	1
2.5	1	4.13	1	8.10	1	11.17	1
2.6*	1	4.14	1	8.12	2	11.18	1
2.8	4	4.15	1	8.14	3	12.13	1
2.14	1	4.15*	1	8.15	1	12.13*	1
2.15	1	4.17	1	8.17	4	12.14	1
2.16	1	4.18*	1	8.17*	1	13.14	1
2.17	1	5.12	1	8.19*	1	13.15	1
2.17*	1	5.13	3	9.11	1	13.16	2
2.18	1	5.14	3	9.12	2	15.17	2
3.4	3	5.15	10	9.13	1	16.17	7
3.5*	1	5.17	1	9.14	8	17.18	1
3.6	2	5.19*	1	9.16	3		
3.8	4	6.7	3	9.19*	1		
3.9	2						

The most frequent and widely distributed Rb chromosomes are 5.15, 10.12, 9.14, 11.13 and 16.17 which were observed in seven or more different karyotypes. Similarly composed metacentrics in karyotypically distinct populations pose the question of whether they are derived by spread from one source or from multiple independent mutational events. Yet, the answer must remain open as long as definitive markers along the Rb chromosomes or genetic tests for the precise ascertainment of identity or diversity are not available. However, from the geographical distribution patterns it can be inferred that spreading of Rb chromosomes is in majority, though not all cases, a likely explanation (GROPP et al. 1982). Even the presence of three similary composed metacentrics in the populations near Zadar (Yugoslavia) and Palermo (Sicily) might be attributable to accidental introduction, e.g. by naval trade routes. It is possible that several new Rb chromosomes arose or accumulated independently after an initial spread of founder Rb metacentrics but a mutual spread between preexisting multimetacentric populations is similary possible. In this respect and with regard to spread by sea traffic, it is interesting to note that the population with metacentric chromosomes near Zadar is limited to a coastal area surrounded by populations with only acrocentric chromosomes (DULIĆ et al. 1980). The origin of mouse populations with Rb metacentric chromosomes outside Italy can be suspected to have

occurred in coastal areas of Greece, Spain, Scotland and Tunesia suggesting accidental spread of Rb translocations into foreign populations via boat traffic. Interestingly Rb chromosomes are frequent in some parts of the British Isles (ADOLPH and KLEIN 1981), which, as proposed by DAVIS (1982), have been settled by continental mice via Vikings. It is likewise conceivable that the mutational events leading to the formation of biarmed chromosomes have taken place under the force of mixed genetic background of local and foreign genes. The finding of a "new" Rb chromosome in a Japanese population that showed signs of contamination with European house mice, is in favour of this hypothesis (MORIWAKI et al. 1984). Although Rb populations of the house mouse occur in many countries in Europe, the accumulation of Rb translocation chromosomes is most advanced in Italy. Altogether 11 populations with seven or more pairs of Rb chromosomes have been described. Similarly high numbers were only occasionally found outside Italy as in Tunesia. Under the viewpoint of time, the origin or introduction of Rb chromosomes in populations outside Italy is supposed to be more recent. This assumption is supported by the fact that the majority of populations with Rb translocations outside Italy, e.g. Greece, Spain, Southern Germany or Scotland is heterozygous or shows only lower numbers of Rb metacentrics. It has been claimed that Rb heterozygosity in natural populations plays an important role as a potent barrier and isolating mechanism between Rb and non Rb containing populations (WHITE 1978). This belief is based on the fact, that after introduction of ferally derived Rb chromosomes into a laboratory mouse genome heterozygous Rb carriers show an impaired fertility (TETTENBORN and GROPP 1970; CATTANACH and MOSELEY 1973; GROPP et al. 1974). This characteristic has been attributed to natural Rb-hybrids as well. The proof of unimpaired fertility of the natural hybrid of Zadar may indicate, that heterozygosity of at least some Rb chromosomes within their environmental genome does not have a negative effect upon fertility that is present after the introduction of the ferally devired Rb chromosome into a laboratory mouse genome (see Table 3). Since at the present time no real proof exists of a detrimental effect of Rb heterozygosity in natural hybrids, the role of chromosomes as an isolating mechanism and hence in the process of speciation has to be reconsidered.

The great number of variable composed Rb chromosomes in natural populations of the house mouse might lead to the assumption of a random involvement of all 19 acrocentric chromosomes of the mouse in the mutational process of Robertsonian centric translocations. Yet, an evaluation of frequency of involvement of each one of the acrocentric elements of the mouse karyotype in the 77 known Rb metacentrics shows (Fig. 3) that some are very frequently represented, as e.g. chromosome 10, 12 and 14, whereas others like no 7 and 18 participate only occasionally in the formation of Rb chromosomes, and chromosome 19 is, at least in feral house mice, never involved as it is with the sex chromosomes. It follows that certain chromosomes are more susceptible for the hypothetical mechanism which induces or facilitates the events of Rb translocations. If this assumption is correct, a sequential order of autosomes involved in Rb translocations has to be postulated. Although there is no definitive way to assess the subsequent changes in Rb accumulating natural populations, the comparison of Rb population with low and high numbers of translocated chromosomes can provide some hints for the elucidation of this problem. For example, Rb chromosomes with autosomes nos. 7 or 18 involved are found mostly in populations with high numbers (8 to 9 pairs) of Rb chromosomes, whereas autosomes 12 and 10 as one arm of a Rb chromosome are represented almost in all Rb-populations, even in populations with low numbers of mutated chromosomes (1 to 3 pairs). Although the numbers of metacentric chromosomes of laboratory mouse strains are low, a similar nonrandom involvement of autosomes does not seem to exist.

What may be the reason for the differential proneness of individual chromosomes of the wild mouse genome to be involved in centric translocations? MILLER et al. (1978) have pointed out that nucleolus organizer regions (NORs) do have some influence upon the

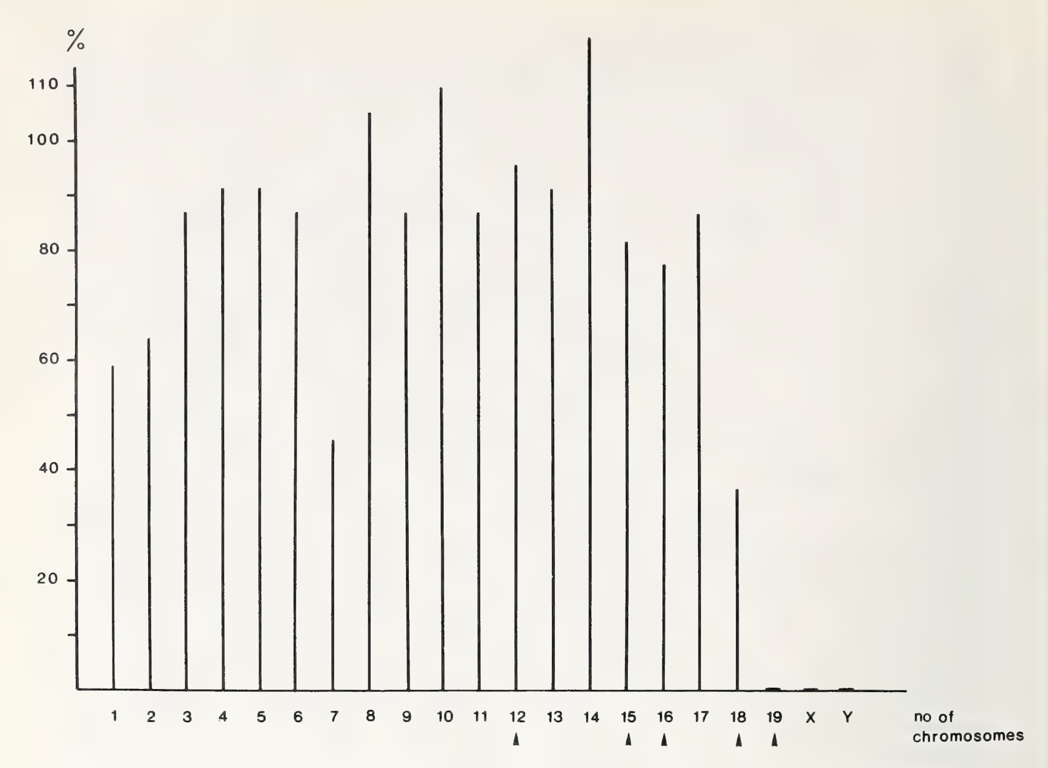


Fig. 3. Percentage of each chromosome of the standard karyotype as one part of individual Rb translocations in different populations of feral mice from Europe and Northern Africa. The calculation is based on data of 22 mouse populations (see Tab. 4 and Fig. 2). Values above 100 % result from multiple involvement of certain autosomes in Rb heterogeneous populations (see Tab. 4, populations 15, 16 and 19). NOR bearing chromosomes are marked with an arrow

frequency of Rb translocations, since in mouse cell lines chromosomes with active NORs are significantly overrepresented in Rb chromosomes. From laboratory mice it is known that chromosomes 12, 15, 16, 18 and 19 may bear NORs proximal to the centromeric heterochromatin. In metaphases of European wild mice silver NORs appear at the same chromosomes and locations, although the presence of silver NORs is variable between feral mouse populations (Winking et al. 1980). The high frequency of chromosomes 12 and 15 in Rb translocations of wild mice supports the data of Miller et al. (1978). However, autosomes 18 and 19 carry silver NORs as well, but are by far the least represented partners in Rb translocations. This may indicate that other factors than NORs play the major role in the production of Rb translocations in feral mouse populations. Additional support of this view comes from the fact that Rb chromosomes with rRNA gene clusters on both sites of the centromere are lacking among the collection of Rb translocations in feral mice. Theoretically the only candidates could have been the combinations 15.17 and 16.17 of European wild mice, but the presence of NORs on chromosome 17 has only been documented in the Asian subspecies *M. m. molossinus* (Dev et al. 1977). A further point, which might be of importance for the generation of Rb chromosomes, is the organization of the region intimately connected with the process of Rb rearrangement. From cytological observations it becomes clear that the breakpoints prior to translocation are located within the paracentromeric heterochromatin or C-band positive material (Gropp and Winking 1981). Heterogeneity of this region in respect of

base pair composition has been ascertained between individual chromosomes of laboratory mice (THUST and RONNE 1980) and chromosomes of mouse cell lines (MARCUS et al. 1980) as well as between species of the genus *Mus* (SEN and SHARMA 1980; BROWN and DOVER 1980). Whether these differences are causally related to the different proneness of chromosomes within the species *Mus* and between species of the genus *Mus* to undergo the process of Rb rearrangement is not yet clear and should be elucidated in further experiments.

Acknowledgement

In memoriam of Prof. Dr. ALFRED GROPP, who discovered the Robertsonian polymorphism of feral mice and made possible these findings.

Zusammenfassung

Karyotypvariation durch Robertsonsche Translokationschromosomen bei der europäischen Hausmaus, Mus musculus. Eine Übersicht über den derzeitigen Wissensstand und neue Informationen

Untersucht wurde der Karyotyp der langschwänzigen Hausmaus, *Mus musculus,* aus Zadar (Jugoslawien) und Ammoudia (Griechenland). In Zadar konnten sechs und in Ammoudia drei Robertsonsche (Rb) Chromosomen nachgewiesen und mit Hilfe der G-Banden identifiziert werden. Die Komposition der Markerchromosomen war teils neu, teils in anderen, geographisch getrennten Populationen schon gefunden worden. Die karyologischen Befunde dieser beiden Populationen aus dem osteuropäischen Verbreitungsgebiet werden gemeinsam mit Beobachtungen zum Karoytyp mittel- und westeuropäischer sowie nordafrikanischer Hausmauspopulationen diskutiert.

Die Fertilitätsdaten eines männlichen Wildfanges mit einer Rb-Heterozygotie lassen den Schluß zu, daß dieser Genotyp in Wildmäusen nicht mit einer Fertilitätseinbuße gekoppelt sein muß, wie sie in Wildmaus/Labormaus-Hybriden infolge von Meiosestörungen mit anschließender Bildung befruchtungsfähiger, aber aneuploider Gameten hinreichend dokumentiert ist.

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Z. Säugetierkunde 53 (1988) 162–169
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ISSN 0044-3468

Sex differences and seasonal variation in habitat choice in a high density population of Waterbuck, *Kobus ellipsiprymnus* (Bovidae)

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Receipt of Ms. 19. 1. 1987

Abstract

Habitat use of waterbuck *(Kobus ellipsiprymnus)* was recorded during road transect counts in Lake Nakuru National Park, Kenya. Waterbuck were encountered significantly more often in open (riverine) forest and open grassland than expected from a random distribution through the available habitat types. There were significant differences in habitat use by different age and sex classes, with the lowest percent overlap (85 %) between adult females and young males. Seasonal differences in habitat use correlated with rainfall: with increasing rainfall waterbuck moved into open grassland, during periods of low rainfall waterbuck moved into open shrub.

Introduction

Waterbuck are antelopes the size of red deer; they occur throughout Africa south of the Sahara (Dorst and Dandelot 1970; Haltenorth and Diller 1977). The two subspecies *Kobus ellipsiprymnus ellipsiprymnus* and *K. e. defassa* interbreed in areas of geographical overlap, e.g. Nairobi National Park, Kenya (Backhaus 1958; Kiley-Worthington 1965). Next to impala (cf. Leuthold 1977; Jarman 1979), waterbuck probably is the antelope species studied most intensively (references in Spinage 1982 and Tomlinson 1980b, 1981; Melton 1983).

The population at Lake Nakuru National Park, Kenya, belongs to the subspecies *K. e. defassa*. With an average of 30 waterbuck per km^2, regionally up to 100/km^2, Lake Nakuru NP has by far the highest density recorded for waterbuck (Kutilek 1974; Wirtz 1978).

The high population density can be expected to have effects on the social behaviour of the species. In three earlier publications (Wirtz 1981, 1982, 1983a) the social behaviour was described. In the following we present data on habitat utilization and on how it varies seasonally and between age and sex classes.

Study area

Lake Nakuru is a shallow alkaline lake at an altitude of 1760 m in the eastern Rift valley, about 130 km northwest of Nairobi, Kenya. Lake Nakuru has become famous as "the lake of a million flamingoes"; up to 1.4 mill. flamingoes have been recorded there (Vareschi 1978). To protect the spectacular avifauna of the lake and its shorelines, the area was declared a bird sanctuary and later a National Park.

A vegetation map of the park is given by Wirtz (1982, fig. 1). Open grassland is dominated by *Cynodon dactylon, Themeda triandra, Chloris gayana,* and species of *Andropogon* and *Hyparrhenia;* near the lake shore the soda-resistant *Sporobolus spicatus* is abundant. Open and dense shrub is formed by patches of *Tarchonantus camphoratus, Lantana trifolia,* and *Pluchea ovalis.* Open and dense forestes are formed by *Acacia xanthophloea, Olea africana* and other *Acacia* species (all species identifications based on Curry-Lindahl [1971] and Kagumaho Kakuyo [1980]). Both study years

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were exceptionally wet years compared to long term means (KUTILEK 1975); see fig. 2 for monthly rainfall values.

The density and biomass of the larger mammals has been described by KUTILEK (1974) and WIRTZ (1978, 1983b). A checklist including the rarer species was given by WIRTZ (1979) and the group size frequencies of the eight most common antelope species was described by WIRTZ and LÖRSCHER (1983). Waterbuck are the dominant larger mammal species in terms of numbers and in terms of biomass.

Material and methods

Field work lasted for 25 months, from November 1977 to December 1979. At the beginning of each month, all roads and tracks of the park were followed with a Landrover. Whenever an individual or a group of waterbuck was seen, the sex and age class of all members of the group and the habitat were noted on a dictaphone. A definition of the age and sex classes used (calves, subadult females, adult females, juvenile males, young males, adult males) is given in WIRTZ (1982). Any waterbuck which could not be assigned to one of the age and sex classes (e.g. because it was partially hidden by the vegetation) was called "unidentified". Counts were made from 7.00 am to 9.30 am and not during heavy rainfall; it took five to seven days to cover the whole park.

The total length of the strip counted in this way was 114 km. Strip width differed according to vegetation. During three of the counts, the distance from the road to each group of waterbuck was estimated, which gives the average sight distance in the different types of habitat. To determine the relative areas of the different habitat types, a separate count was made: While driving the Landrover at a constant speed of 20 mph, the type of habitat to the left and to the right was noted every 2 seconds. The proportion of each habitat along the counting strip multiplied with the average sight distance gives a measurement of the relative sizes of the areas: Table 1.

Table 1. **Relative size of the different types of habitat along the counted transect**

habitat type	proportion along the counting strip (% of records)	average sighting distance (m)	relative size of counting area (% of total)
open grass	33.39	107.89	53.46
dense shrub	12.67	22.83	4.29
open shrub	31.86	57.67	27.27
dense forest	5.03	30.00	2.24
open forest	14.15	45.21	9.50
others	2.90	75.17	3.24

For most of the variables described in the "Results' section, we have used the data for a "representative year" from August 1978 to July 1979 (n = 3017 groups, cumulative number of animals recorded 17064).

Results

Population composition and an estimate of the variance produced by the counting method

Table 2 shows the average population composition for the year August 1978 to July 1979. About a third of the population consisted of adult females. The sex ratio of adult and subadult animals was not significantly different from 1:1 (50.7 % ♂♂ : 49.3 % ♀♀;

Table 2. **Population composition (annual mean)**

	adult males	young males	juvenile males	adult females	subadult females	calves	unidentified
n seen in the 12 counts	3253	3068	987	5353	1830	1055	1518
% (mean of the monthly percentages)	19.1	18.0	5.8	31.4	10.7	6.2	8.8

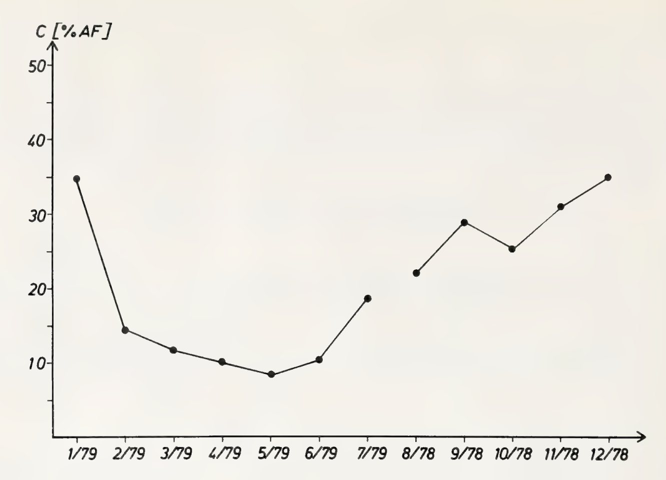


Fig. 1. Monthly variation in the number of calves per hundred adult females

$p > 0.2$, t-test). The sex ratio of adult animals was 1:1.6 (♂♂ : ♀♀). The percentage of calves in the population varied from 2.9 (June) to 9.7 (December); fig. 1 shows the numbers of calves per hundred adult females during the course of the year.

How accurate are the monthly counts? A second count was begun immediately after the first one in June 1979 and in September 1979. Table 3 compares the results. Even though

Table 3. **Comparison of the results of two consecutive counts**
(percent of each age class in the total)

	adult males	young males	juvenile males	adult females	subadult females	calves	unidentified	n animals
June 79–A	19.4	18.6	6.5	35.0	10.9	2.9	6.7	1576
June 79–B	19.3	21.8	7.5	31.5	11.0	4.1	4.9	1282
Sept. 79–A	16.0	23.4	5.5	34.6	8.2	5.9	6.4	1571
Sept. 79–B	16.2	17.6	4.1	38.8	9.5	6.8	7.1	1629

the absolute number of animals counted during the first and second count can differ by as much as 300, the percentage of each age class in the total was very similar in the two counts made during the same month. The counting procedure apparently gives well-reproducible results.

Habitat utilization

General pattern

Table 4 compares the relative frequencies of habitat types availabe (from table 1) and the proportions of waterbuck counted in them during the 12 months. Most of the habitat covered during the counts consisted of open grassland and most waterbuck were seen in open grassland. However, waterbuck were not evenly distributed throughout the available habitat types: a larger proportion of waterbuck was seen in open grassland than expected for an even distribution ($p < 0.001$, chi-square test).

Table 4. **Habitat availability and the proportion of waterbuck seen in the different types of habitat**

	open grass	open shrub	dense shrub	open forest	dense forest	others
proportion of animals counted (n=17064)	57.2	21.4	4.5	15.5	0.7	1.0
relative size of area	53.5	27.3	4.3	9.5	2.2	3.2

Age and sex specific trends

There were sex differences and age differences in the distribution of waterbuck: Table 5.

The distribution of each age class differs with $p<0.001$ from an even distribution through the available habitat types (chi-square test). A considerably larger proportion of adult males was seen in open grassland than expected for an even distribution (compare

Table 5. **Percentage of different age classes and sexes in the different types of habitat (annual mean)**

	adult males	young males	juvenile males	adult females	subadult females	calves	unidentified
open grass	64.56	59.21	50.99	50.55	51.78	56.88	69.40
open shrub	19.27	26.38	29.74	20.11	20.15	17.68	19.94
dense shrub	2.54	2.56	5.05	5.92	5.11	4.02	3.88
open forest	12.50	11.03	13.18	20.58	20.45	19.57	6.10
dense forest	0.49	0.27	0.49	1.32	0.73	0.96	0.27
others	0.65	0.56	0.56	1.52	1.79	0.89	0.41
n animals	3253	3068	987	5353	1830	1055	1518

with lower part of table 4). In contrast, adult females were seen in open grassland less often than expected and in open forest much more often than expected. The difference in distribution pattern of adult males and adult females is significant with $p<0.001$ (chi-square test).

A comparison of the different age classes shows how the sex-specific distribution pattern becomes more pronounced from calf to adult animal. Calves (which remain hidden during the first two to four weeks of their life; SPINAGE 1982) were seen in open shrub and open forest more often than expected for an even distribution. The distribution of subadult females has shifted to an even stronger preoponderance in open shrub and open forest (comparison with calves: $0.10p<p<0.05$, chi-square test). Compared to subadult females, adult females were found more often in dense shrub and approximately equally often in open shrub and open forest ($0.2< p<0.1$). The distribution patterns of calves, juvenile males, young males, and adult males differ significantly ($p<0.001$) in each comparison: with increasing age the males change from open forest, dense shrub and open shrub to open grassland.

A numerical expression of similarity (or difference) in habitat utilization is given in the percent overlap. For each class, the proportion using the different habitat types is calculated (i.e. table 5); then the lower of the two percentages of the classes that are compared is summed over all habitat types to give the percent overlap. Table 6 shows the results: the highest overlap in habitat use (98.5 %) was between adult females and subadult females, the lowest overlap (85.1 %) was between adult females and young males. The average overlap in habitat use of classes belonging to the same sex (92.5 %) is higher than the average overlap of classes belonging to a different sex (87.5 %).

Table 6. **Percent overlap in habitat use**

	adult males	young males	juvenile males	adult females	subadult females	calves
adult males	100					
young males	92.9	100				
juvenile males	86.8	91.8	100			
adult females	86.0	85.1	89.9	100		
subadult females	87.2	86.3	90.4	98.5	100	
calves	90.7	89.0	86.9	93.7	94.7	100

Seasonal variation

From month to month, there could be large differences in the proportion of waterbuck counted in the same habitat. Fig. 2 illustrates this by showing the percentage of adult females counted in open grass and in open shrub from August 1978 to July 1979; between

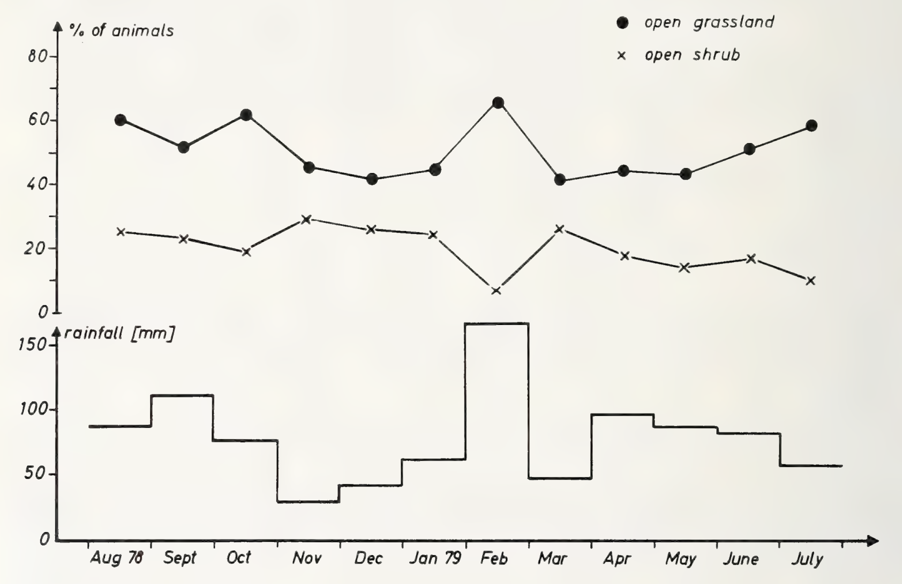


Fig. 2. Monthly variation in the percentage of adult females in open grassland and in open shrub and monthly variation in rainfall

7 % and 30 % of the adult females were counted in open shrub and between 41 % and 66 % in open grassland. For a total of 15 months, there were data on rainfall and on habitat use (habitat was unfortunately not recorded during all of the road strip counts). Rainfall and habitat use correlate in the following way: there was a negative correlation between the amount of rain falling in a month and the percentage of animals counted in open shrub ($p < 0.05$ for all animals and for adult females alone, Spearman rank test); there was a positive correlation between the amount of rain falling and the percentage of animals counted in open grassland ($0.1 > p > 0.05$ for all animals and $p < 0.05$ for adult females alone, Spearman rank test); there was no discernible correlation between the amount of rain falling in a month and the percentage of animals counted in dense shrub, dense forest,

and open forest. With decreasing rainfall the proportion of waterbuck counted in open grass decreased and the proportion of waterbuck counted in open shrub increased. Note that the second statement is not a necessary consequence of the first statement but a separate finding: animals leaving open grass areas could have dispersed into several other types of habitat. With increasing rainfall waterbuck moved from open shrub to open grassland, with decreasing rainfall waterbuck moved from open grassland to open shrub.

There is no definite calving season in Nakuru waterbuck; newborn calves were seen throughout the year. The percentage of calves counted did, however, increase sharply during July to September (fig. 1). We tested whether adult females, in any month, changed habitat use in a different direction than did adult males. While there were differences in the degree of change in habitat use, the directions of shift of adult females and of adult males resembled each other and corresponded to the pattern shown in fig. 2.

Discussion

Waterbuck depend on permanent access to water; they almost completely lack the ability to reduce water loss in response to a shortage of water (Taylor et al. 1969) and they tend to occur close to areas where water is readily available (e.g. van Lavieren and Esser 1979; Spinage 1982; Sinclair 1985). In Nakuru National Park nearly all areas covered during the counts, including "open grassland", were within three kilometres' distance to water and most of the "open forest" was forest along rivers draining into Lake Nakuru. Due to the exceptional amounts of rain during the study period, the waterholes were always full.

Waterbuck groups are open groups; they continuously change their size and composition. From a group in, for instance, open grassland some animals may wander off into adjacent forest, while others from nearby open shrub may join those in grassland. Individuals apparently make an independent choice and the number of animals (instead of the number of groups) in a certain habitat has therefore been used as a measure of habitat utilization.

Statements on habitat use of waterbuck in the literature are sometimes based on the proportion of animals seen in different types of habitat but without relating these proportions to the relative areas available (e.g. Spinage 1982). In the most extensive study of antelope-habitat relationships, Hirst (1975) showed that the waterbuck of the Transvaal lowveld (South Africa) occured in riverine gallery forest more often than expected for an even distribution through available habitat types. No preference for open grassland was indicated in Hirst's study. Caution must be used in the interpretation of such differences between study areas because the nature of the habitat described with the same name may differ in subtle ways which are nevertheless important to the animals. Whereas most of the Nakuru grassland was close to water, the grassland in Hirst's study area may not have been. Jarman (1972) and Sinclair (1985) also found a preference of waterbuck for riverine forest and for grassland in the Zambezi valley and in Masai Mara National Park.

Different visibility of the different age classes may have affected the counts and the apparent age differences could be an artefact. However, only for calves is this likely to be true: in dense habitat calves are more likely to be overlooked than larger animals and this may have resulted in an overestimate of the proportion of calves in open habitat.

We assume that the pattern of habitat use shown by the animals is adaptive, i.e. that animals using certain habitat types at a given time have a higher chance of survival and/or reproductive success. Food, predation and climate are the factors most likely to be of importance (but see Peek et al. 1976 for an example of the influence of parasites). Differences in habitat utilization between age and sex classes can be due to differences in their requirements and/or to different action of external variables. Seasonal differences can be due to changes in requirements and/or changes in external variables.

Except for occasional predation on calves by leopards, there was no predation on Nakuru waterbuck. Females spent most of their time inside territories (along the lake shore and along rivers) where the grass appeared to be greener and lusher than in open grassland further away from water (but no measurements of the nutritionally relevant components were taken). Females also spent more time feeding than did males (WIRTZ and OLDEKOP, in prep.). Forage quality appeared to be the main factor governing the distribution of the females.

The nutritional value of many forage species varies greatly with the available moisture. Ungulates require on average 4–5 % crude protein in their diet, but the crude protein content of grass drops from about 8 % in the wet season to 1–3 % in the dry season (SINCLAIR 1975; AFOLAYAN and FAFUNSHO 1978). Large scale migrations of ungulates, e.g. the spectacular migration of wildbeest, seem to be a response to forage quality and quantity. Small scale shifts in habitat utilization of nonmigratory African ungulates, such as those shown by Nakuru waterbuck, are probably an analogous process (KUTILEK 1979).

"Choice" may be the wrong word to describe the process regulating the distribution of part of the male population. Territory holders excluded most of the remaining adult males and most of the young males from their territories (WIRTZ 1982). Analysis of faeces of waterbuck in Rhodesia (TOMLINSON 1980a, 1981) and the time budgets of the Nakuru waterbuck (WIRTZ and OLDEKOP, in prep.) indicate that bachelor males are relegated to nutritionally inferior areas. Probably, only a small portion of the adult male population was actually in the preferred location and the sex differences in habitat use were caused by the action of the territorial males that kept most of the male population out of the areas the females used for foraging. Differential distribution of males and females caused by the territorial behaviour of some of the males has been described for several other antelope species and JARMAN and JARMAN (1973) suggested that, as a consequence, females benefit by an enhanced resource apportionment which might even lead to an increase in calf production.

Acknowledgements

The data were collected while the senior author held a postdoctoral grant of the Max-Planck-Gesellschaft; the Kenyan Government gave research permit OP 13/7C245/4; as a voluntary field assistant, ANDREW BARTON assisted during several of the counts. Many thanks to them.

Zusammenfassung

Geschlechtsunterschiede und jahreszeitliche Variation in der Habitatwahl in einer Hochdichte-Population des Wasserbocks (Kobus ellipsiprymnus)

Bei Transekt-Zählungen im Nakuru Nationalpark, Kenya, wurde registriert, wie häufig Wasserböcke *(Kobus ellipsiprymnus)* in den verschiedenen Habitaten gesehen wurden. Wasserböcke wurden signifikant häufiger in offenem flußnahem Wald und in offenem Grasland gesehen als dies bei einer gleichförmigen Verteilung über die vorhandenen Habitate zu erwarten war. Die Habitatnutzungsmuster verschiedener Altersklassen und der beiden Geschlechter waren signifikant voneinander verschieden. Die geringste Überlappung in der Habitatnutzung (85 %) war zwischen adulten Weibchen und jungen Männchen. Die saisonalen Unterschiede korrelierten mit der Regenmenge: bei hohen Niederschlagswerten hielten sich die Wasserböcke häufiger in offenem Grasland auf, bei niedrigen Niederschlagswerten mehr in offenem Buschland.

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Z. Säugetierkunde 53 (1988) 170–177

ISSN 0044-3468

Summer food habits and quality of female, kid and subadult Apennine chamois, *Rupicapra pyrenaica ornata* Neumann, 1899 (Artiodactyla, Bovidae)

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Receipt of Ms. 06. 01. 1987

Abstract

Investigated the summer diet of a flock of the Apennine chamois comprising females, kids and subadults. Monthly observations were carried out between June and September from 1982 to 1984. The study area consisted of grasslands above the timberline belonging to the *Festuco-Trifolietum thalii* plant community, in the upper Val di Rose (Abruzzo National Park, Italy). Our data were obtained from direct observations of grazing animals and from an analysis of the plants browsed. From June to September about 70 % of the total number of species are grazed. However the composition of the diet shows monthly shifts conditioned by the grassland phenology and the grazing selection. A tentative estimate of the main chemico-nutritional features of the diet suggests that the grazing selection keeps the *Festuco-Trifolietum thalii* suitable to supply a protein-rich and fibre-poor diet during the whole summer.

Introduction

The quality and availability of food, together with security aspects, determine the habitat quality for the chamois (Schröder 1971; Elsner-Schack 1985).

While in the north-eastern chamois populations *(Rupicapra rupicapra)* this fact has been extensively studied (see Lovari 1985 for a review), very little is known on the food ecology of the south western species *(Rupicapra pyrenaica)*.

In this paper we give some detailed data on the summer diet of females, kids and subadults of the Apennine subspecies of the south western chamois (*Rupicapra pyrenaica ornata;* Nascetti et al. 1985).

The only remaining population of this subspecies can be found in some mountains in the central Apennines of the Abruzzo National Park (Italy). Holocene remains and historical sources demonstrate a wider range in the central and southern Apennines up to historical times (Masini 1985).

As for studies on the diet of the alpine chamois (e.g. Onderscheka 1974; Dunant 1977; Schröder 1977) and of the Pyrenean one (Berducou 1975; Garcia-Gonzales 1984) these data will provide a background towards clarifying the environmental requirements of this "vulnerable" ungulate (Thornback 1980) and towards ensuring the success of possible reintroductions.

Study area and methods

The study area lies in the upper Val di Rose (Abruzzo National Park, Italy), between Mount Sterpalto (1966 m) and Mount Boccanera (1982 m). This area is part of the Camosciara mountains which are the core of the chamois range in the National Park. Breaches formed by white and grey Dolomitic limestones dating from the Lias characterize the landscape (Praturlon 1968). A mixed beach forest covers the slopes of the mountains up to about the timberline (1700–1800). According to the

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phytosociological approach (Braun-Blanquet 1964) the alpine grasslands belong to the vegetation types *Festuco-Trifolietum thalii* and *Avena versicolor-Koeleria splendens* community. Only the former is intensively grazed in summer by flocks of females, kids and subadults; the latter is grazed by solitary adult males. We therefore concentrated our observations on the *Festuco-Trifolietum thalii.* The plant community was sampled with the phytosociological method (Braun-Blanquet 1964) and the cover of the species was estimated in a simplified way as 3: beyond 2/3, 2: from 1/3 to 2/3; 1 up to 1/3 of the minimal area of the relevé. The sampling of the grazed species was carried out by direct observations. Our data were collected monthly for three years (1982 to 1984), from June to September, except for August (1983). The seasonal period we considered corresponds at first to the lactation and then (August-September) to the early weaning of kids. The flocks were observed using 12 × 50 binoculars from a distance of about 30–40 m. For each of the grazed species, the parts of the plant were noted (F: flowers; L: leaves; Fr: fruits), and the average grazing frequency (g.f.) was estimated (3: beyond 2/3; 2: from 1/3 to 2/3; 1: up to 1/3), using a slight modification of the scale proposed by Dunant (1977). Nomenclature of taxa follows Pignatti (1982), except for *Graminaceae* (Tutin et al. 1964–80). A tentative estimate of the chemical composition of the diet was carried out by analysing 100 g samples of the monthly diet. The grazed parts of the plants were weighted on the basis of species cover in the phytosociological relevés. For each species and each month the calculation was as follows:

$$\text{Grazed part weight (g)} = \frac{\text{Part grazing frequency} \times \text{species cover}}{\text{Total grazing frequency} \times \text{Total species cover}} \cdot 100$$

The values we have considered in the calculation are in Table 1. Samples were weighed on a digital portable balance. They were sealed under vacuum in plastic containers and maintained at 0 °C until analysing.

The samples were dried in a forced ventilation heater at a temperature of 65 °C up to constant weight. The content of crude protein, calcium, phosphorus, magnesium (A.O.A.C. 1984) and cell wall constituents (NDF; Goering and Van Soest 1970) were determined.

Results

The specific composition and phenology of diet

The sampled species are listed in Table 1. There are 54 grazed species; the total number of species is 78. This means that, during the observation period, the flocks grazed 69.2 per cent of the total number of species.

The specific composition of the grasslands is that of the vegetation type *Festuco-Trifolietum thalii,* here characterized by *Festuca violacea macrathera, Trifolium thalii, Crepis aurea glabrescens* and *Plantago atrata.*

Considering as available only those species which, in each month, were at phenological phases unlike "seedling" or "dried plant", we can see (Fig. 1) that the number of available species is lowest in June, and is almost constant from July to September. Ratios between grazed species and available species show no significant differences during the whole summer.

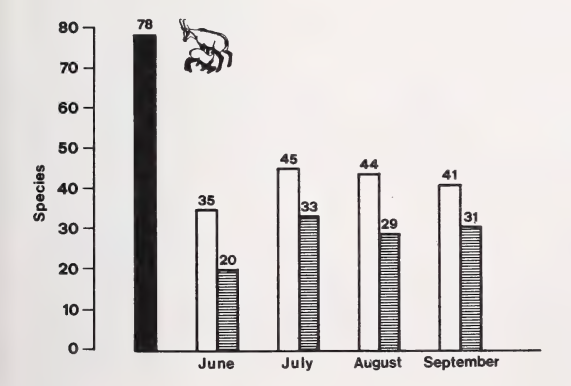


Fig. 1. Number of grazed species (striped column) during the summer in relation to the total number of species (black column) and the available species (white column). Monthly ratios between grazed and available species are the following: June: 0.57; July: 0.73; August: 0.66; September: 0.76. Grazed species are listed in Table 1; available species in Table 2. (Further explanations in the text)

Table 1. ***Festuco-Trifolietum thalii***

Grazed species

Species	June		July		Aug.		Sept.	
	F	L	F	L	F	L	F-Fr	L
Aspidiaceae								
Polystichum lonchitis (1)		3		3				
Campanulaceae								
Phyteuma orbiculare (1)			1					
Chenopodiaceae								
Chenopodium bonus-henricus (1)			2	2	2	2	2	2
Compositae								
Achillea millefolium (1)					1			
Adenostyles australis (1)			3	3				
Aster bellidiastrum (2)	3	3	2					2
Bellis pusilla (1)	3	3	2	2		2		3
Carduus carlinaefolius (1)			1	1				
Chrysanthemum tridactylites (1)			2	2				
Cirisum eriophorum (1)			1				2	
Crepis aurea glabrescens (3)		2	3	3		2	3	3
Doronicum columnae (1)	3		3			1		2
Leontodon hispidus (1)								1
Senecio rupestris (1)			1				1	
Taraxacum officinale (2)		2	2	3	3			
Cruciferae								
Arabis alpina caucasica (1)			1	1				
Cupressaceae								
Juniperus nana (1)		2						
Gentianaceae								
Gentiana lutea (1)		3		2		3		
Geraniaceae								
Geranium cinereum (1)								3
Geranium macrorrhizum (1)								3
Graminaceae								
Festuca dimorpha (1)						3		
Festuca nigrescens (1)	3	3	2			2		2
Festuca robustifolia (1)	3	3				3		2
Festuca violacea macrathera (2)		3		1		3		
Phleum alpinum (1)						1		
Poa alpina (2)	2	2	2	2		2		
Juncaceae								
Luzula sieberi (2)						3	2	2
Leguminosae								
Anthyllis vulneraria group (1)			2					
Astragalus depressus (1)							2	2
Medicago lupulina (1)						1		
Trifolium pratense semipurpureum (1)	1			2	1	1	2	2
Trifolium repens (1)							2	2
Trifolium thalii (3)	2	2	3			3	3	3
Liliaceae								
Veratrum album lobelianun (1)			2	2		3		1
Orobanchaceae								
Orobanche sp. (1)							1	1
Plantaginaceae								
Plantago atrata (3)	3	3	2	2		3		3
Plumbaginaceae								
Armeria majellensis (1)			1			2		2
Polygonaceae								
Rumex acetosa (2)	3		3	3			3	3
Primulaceae								
Soldanella alpina (1)						2	1	1

Table 1 (continued)

Species	June		July		Aug.		Sept.	
	F	L	F	L	F	L	F-Fr	L
Ranunculaceae								
Pulsatilla alpina alpina (1)					3	3		
Ranunculus apenninus (2)	2	2	1			2	2	2
Rubiaceae								
Galium anisophyllum (1)			1					
Scrophulariaceae								
Linaria purpurea (1)							1	
Pedicularis comosa (1)						3		
Rhinanthus alectorolophus (1)					1	1	1	1
Scrophularia scopolii (1)	1	1			1			
Verbascum longifolium (1)		1						2
Thymelaeaceae								
Daphne mezereum (1)							1	2
Umbelliferae								
Chaerophyllum hirsutum hirsutum (1)			1	1	3	3		
Chaerophyllum hirsutum magellense (1)			1	1		3		
Heracleum pyrenaicum orsini (2)		3	3	3		3	2	2
Pimpinella alpestris (1)			3	3				
Valerianaceae								
Valeriana montana (2)			3				3	
Violaceae								
Viola eugeniae eugeniae (1)			1				1	

Mean cover (within brackets): 1 = up to ⅓; 2 = from ⅓ to ⅔; 3 = beyond ⅔. Grazed parts: F = flowers; L = leaves; Fr = fruits. Grazing frequencies: 1 = up to ⅓; 2 = from ⅓ to ⅔; 3 = beyond ⅔. Further explanations in the text.

Table 2. **Festuco-Trifolietum thalii**

Available ungrazed species in each month

June (15)	Compositae: *Gnaphalium diminutum, Chrysanthemum tridactylites, Senecio rupestris, Taraxacum officinale*; Cruciferae: *Erysimum majellensis*; Gentianaceae: *Gentiana nivalis*; Labiatae: *Stachys alopecurus divulsa; Thymus serpyllum* group; Plumbaginaceae: *Armeria majellensis*; Primulaceae: *Soldanella alpina*; Ranunculaceae: *Pulsatilla alpina*; Rosaceae: *Alchemilla nitida*; Rubiaceae: *Galium anisophyllum*; Scrophulariaceae: *Scrophularia scopolii*; Umbelliferae: *Pimpinella alpestris.*
July (12)	Boraginaceae: *Myosotis alpestris*; Compositae: *Achillea millefolium, Carduus chrysacanthus*; Cupressaceae: *Juniperus nana*; Geraniaceae: *Geranium cinereum, Geranium macrorrhizum*; Labiatae: *Lamium maculatum, Thymus serpyllum* group; Primulaceae: *Soldanella alpina*; Rosaceae: *Alchemilla nitida*; Scrophulariaceae: *Scrophularia scopolii, Verbascum longifolium.*
August (15)	Aspidiaceae: *Polystichum lonchitis*; Campanulaceae: *Campanula scheuchzeri*; Caryophyllaceae: *Cerastium tomentosum*; Convolvulaceae: *Cuscuta* sp.; Cupressaceae: *Juniperus nana*; Cyperaceae: *Carex kitaibeliana*; Graminaceae: *Dactylis glomerata, Bromus erectus*; Labiatae: *Thymus serpyllum* group; Rubiaceae: *Asperula aristata, Galium anisophyllum*; Scrophulariaceae: *Linaria purpurea, Verbascum longifolium*; Umbelliferae: *Seseli libanotis*; Urticaceae: *Urtica dioica.*
September (10)	Aspidiaceae: *Polystichum lonchitis*; Caryophyllaceae: *Cerastium tomentosum*; Compositae: *Achillea millefolium, Carduus chrysacanthus, Taraxacum officinale*; Cupressaceae: *Juniperus nana*; Juncaceae: *Juncus monanthos*; Labiatae: *Stachys tymphaea*; Santalaceae: *Thesium parnassi*; Urticaceae: *Urtica dioica.*

Nevertheless, if we compare two by two the monthly lists of grazed species (Table 1) through their common species and their species restricted to one month, we can see that the floristic composition of the diet shows a significant difference between June and July (χ^2 = 3.94 with 1 df, and significant at P = 0.05).

In Table 1 we also can see that: only the flowers of the species *Phyteuma orbiculare, Achillea millefolium, Cirsium eriophorum, Senecio rupestris, Anthyllis vulneraria* group, *Galium anisophyllum, Linaria purpurea, Valeriana montana, Viola eugeniae* subsp. *eugeniae* are eaten. 9 species altogether.

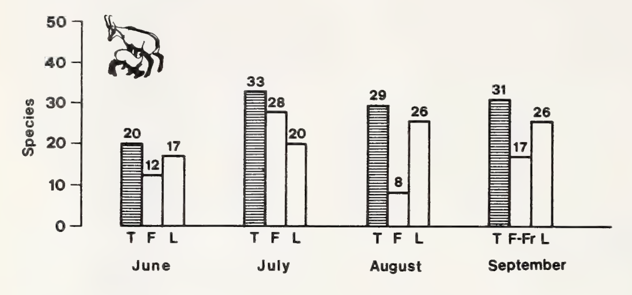


Fig. 2. Number of grazed species (T) subdivided according to parts eaten. F = flowers; Fr = fruits; L = leaves

Only the leaves are grazed in the following species: *Polystichum lonchitis, Gentiana lutea, Geranium macrorrhizum, Festuca dimorpha, Festuca violacea* subsp. *macrathera, Phleum alpinum, Medicago lupulina, Juniperus nana, Pedicularis comosa, Verbascum longifolium, Daphne mezereum.* 11 species in all.

The other grazed species (34) are subjected to an indiscriminate form of grazing.

Fig. 2 shows that in July there is a clear preference for flowers. From July to August there is a marked decrease in the grazing of flowers. (χ^2 = 18.50 with 1 df, highly significant). Leaves are grazed with high frequency during the whole observation period.

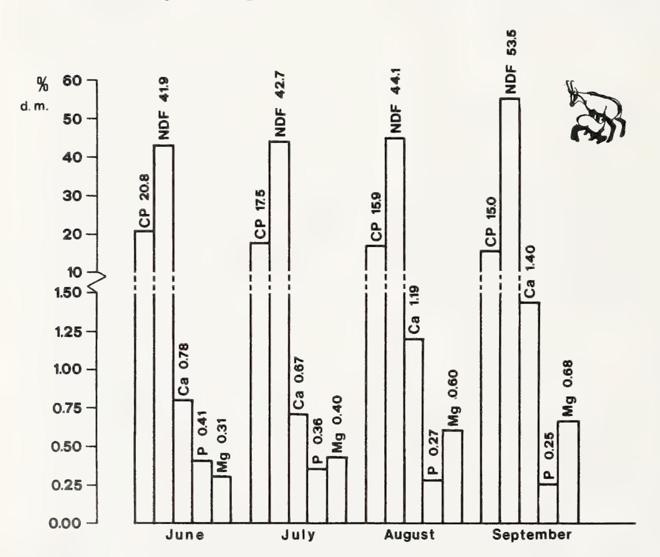


Fig. 3. The main chemico-nutritional features of the summer diet. Monthly per cent content on the dried matter (d. m.) of crude protein (CP), cell wall constituents (NDF: neutral detergent fiber) and some elements. (Further explanations in the text)

The main chemico-nutritional features of the diet

Fig. 3 shows the results of our tentative estimate of some chemico-nutritional features of the diet. The differences between our monthly data have no statistical significance. However, their apparent trends suggest a decrease in the crude protein (CP) and phosphorus content of the diet and an increase in cell wall constituents (NDF), calcium and magnesium, from June to September.

Discussion

The grassland grazed in summer by females, kids and subadults of the Apennine chamois belong to a vegetation type *(Festuco-Trifolietum thalii)* which is common in the alpine vegetation belt of the Alps, but is rare and extrazonal in the high mountains of northern and central Apennines (Pignatti 1979). Some significant subspecies such as *Festuca violacea* subsp. *macrathera* and *Crepis aurea* subsp. *glabrescens* indicate a slight chorological difference between the Apennine community and the *Festuco-Trifolietum* described for the Alps (Braun-Blanquet 1949–50). As in the Alps its distribution is restricted to sites with a long-lasting snow covering and weakly acid soils. In the Abruzzo National Park, such environmental conditions occur in some northern slopes of the Camosciara mountains – which include the upper Val di Rose – but are rare and fragmentary elsewhere, as, for instance, on Mount Amaro (1862 m). The striking difference between the great number of chamois in the Camosciara with respect to other Park areas could be explained on the basis of the importance of the *Festuco-Trifolietum thalii* as a food source especially during lactation. The phenology of this plant community has a role in determining the grazing habits of females and subadults and some nutritional shifts in the diet.

From June to September the increase of magnesium (from leaves) and the decrease of phosphorus (from flowers), as our data indicate, are well known phenologically related facts.

The high values found in June in the phosphorus content of the diet (0.42 % of the d. m.) may be related to the corresponding chamois preference for the floral parts of plants. Moreover, it is well known that grasses and many other plants show decreasing phosphorus contents evolving from the early stage (0.40 % of the d. m.) to the end of flowering (0.20 % of the d. m.; Bouquet and Gueguen 1979).

On the contrary, the phenologic decrease of proteins (from young leaves and flowers) corresponds to only an apparent slight decrease of protein content in the diet. As suggested by Fig. 4, this fact may be well explained on the basis of an increasing grazing frequency of Leguminosae leaves from June to September. The proteins of these leaves have a high digestibility and exercise a stimulating effect on the rumination (Grenet and Demarquilly 1977). In *Trifolium repens* Ulyatt (1981) observed a good digestibility even in an advanced vegetative state, as the herbivores only graze the leaves and the leaf-stalks of this clover. This removal should provoke a regeneration of a new leaf tissue which would keep up the supply of low fibre content forage but with high protein content.

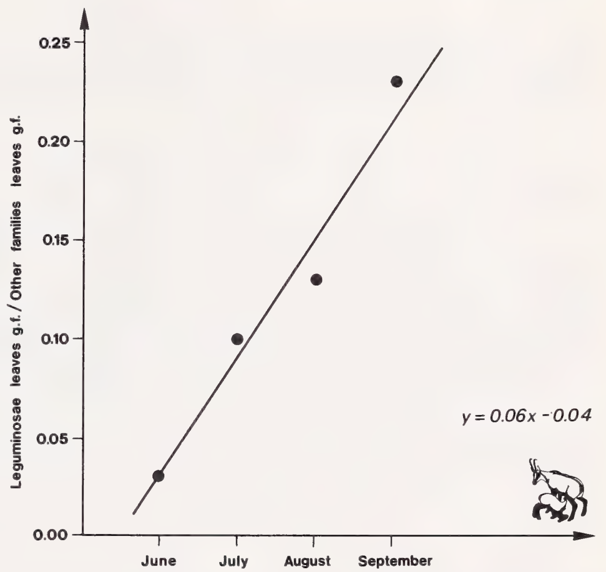


Fig. 4. Monthly ratios between the grazing frequency of Leguminosae leaves and the grazing frequency of leaves of other families. Grazing frequencies (g. f.) are estimated according to Dunant (1977), modified. June: 0.03; July: 0.10; August: 0.13; September: 0.23. The correlation coefficient r = 0.98, with 1 df, is highly significant

A similar situation could come about in the *Festuco-Trifolietum thalii*, where *Trifolium thalii* and other Leguminosae are abundant and are intensely browsed (see Table 1). In the same seasonal period the apparent increase in calcium content can be accounted for in the same way, i.e. on the basis of the increased browsing of the leaves of the Leguminosae (Van Soest 1982). Finally, the diet presents fairly constant fibre values, at least up to the whole of August. The animals' careful grazing selection may have contributed to this phenomenon, as they choose the less fibrous parts of plants. This last aspect has been highlighted in the alpine chamois (Drescher-Kaden 1981).

Our results based on the analysis of a diet reconstructed by browsing data, need a confirm from more accurate investigations. However they suggest for the Apennine chamois what is already known in general for other ruminants (Arnold 1981): the grazing selection tends towards obtaining protein-rich diets which are however poor in fibres.

In conclusion, two results of our studies are to be emphasized: 1. In the late spring (June), summer (July-August) and early autumn (September), the females, kids and subadults of the Apennine chamois seem to depend mainly on a rare and extrazonal plant community in the Apennines, such as the *Festuco-Trifolietum thalii.*

2. The chamois grazing selection keeps this vegetation type suitable to supply a protein-rich diet in a seasonal period which corresponds to the lactation and to the early weaning of the kids.

Acknowledgements

We wish to thank the Direction of the Abruzzo National Park for providing practical facilities in the course of our research. We are also grateful to S. Lovari for the critical reading of the manuscript. The research was partly supported by a grant from the Italian Ministry of Education.

Zusammenfassung

Beschaffenheit und Qualität der Sommernahrung von Weibchen, Kitzen und Subadulten der Apenningemse, Rupicapra pyrenaica ornata Neumann, 1899 (Artiodactyla, Bovidae)

In den Monaten Juni bis September 1982–1984 wurden im oberen Val di Rose (Abruzzen-Nationalpark, Italien) an einer Herde von Apenningemsen (Weibchen, Kitze, Subadulte) monatliche Beobachtungen durchgeführt, um über die Sommernahrung Aufschluß zu erhalten. Die Vegetation im Untersuchungsgebiet oberhalb der Baumgrenze besteht aus Weiderasen *(Festuco-Trifolietum thalii).* Unsere Ergebnisse basieren auf Direktbeobachtungen der äsenden Gemsen sowie auf Analysen der aufgenommenen Pflanzen. Von Juni bis September werden ungefähr 70 % der vorhandenen Pflanzenarten abgegrast, doch die Phänologie des Weiderasens hat großen Einfluß auf die Nahrungswahl. Abschätzungen von chemischer Eigenschaft und Nährwert der Nahrung weisen darauf hin, daß das *Festuco-Trifolietum thalii* sich durch selektives Abweiden als geeignet erweist, eine proteinreiche und faserarme Nahrungsquelle während des ganzen Sommers zu liefern.

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Z. Säugetierkunde 53 (1988) 178–187

ISSN 0044-3468

An annual rhythm in reproductive activities and sexual maturation in male Japanese serows *(Capricornis crispus)*[1,2]

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Receipt of Ms. 2. 1. 1987

Abstract

Changes in reproductive activities were examined in male Japanese serows captured in December to March, 1982 to 1985, in Gifu Prefecture. Examinations were conducted on the spermatogenic activity, testosterone and androstenedione levels in tissue as well as in serum and fructose concentration in the seminal vesicle. In fully adult males over 2.5 or 3 years of age, the highest values in every examination were nearly always found in December. From December to March, the values showed a decided tendency to decrease. A highly significant correlation was found, respectively, between the spermatogenic activity and the testosterone level, and between the fructose content and the testosterone level. These results indicate the presence of an annual rhythm in the reproductive activity in males of this species.

In young animals, the spermatogenic activity, testosterone levels, and fructose contents progressed increasingly with age and attained the adult levels at the age of 2.5 to 3. The concentration of androstenedione in serum of youngs showed the same level as in adults, and there was no definite tendency to decrease associated with sexual maturation.

Introduction

Until our first published study on spermatogenesis in Japanese serows (Tiba et al. 1981a, b), there had been no information available concerning reproductive physiology in males of this species, though it had been known from a few works on sexual behaviour in males, that mating occurs most frequently in October and November (Akasaka 1979; Akasaka and Maruyama 1977). As for females, several important facts had been collected about reproductive activities (Ito 1971; Komori 1975): A single young was born usually from March to June, sometimes in September but seldom in October, the first parturiton in adult females occurred usually at 3 years of age; and the gestation period was 211–213 days in captivity.

From our previous studies mentioned above, it was strongly suggested that reproductive activities in the male are subject to seasonal fluctuations; that is, in fully adult males over 2.5 or 3 years of age, the spermatogenic activity became lower from December to March of every year. It was also clarified in the previous studies that the first appearance of spermatozoa in the seminiferous tubules occurs within 6 or 7 months after birth.

The main purpose of this study is to demonstrate the presence of an annual rhythm in the testicular endocrine function in correlation with the spermatogenic activity as well as the secretory function of fructose from the seminal vesicle, which is a reliable indicator of testicular endocrine function. Another purpose is to determine exactly the completion of sexual maturation in males.

[1] Presented in part at the International Symposium on *Capricornis* and Its Related Species, Komono, Mie Prefecture, Japan, May 1986. – [2] Supported by Grants-in Aid for Co-operative Research (58362001 and 61560338) from the Ministry of Education, Science and Culture, Japan.

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Materials and methods

Examination items and the number of animals used are shown in Table 1. From 1982 to 1985, materials for these examinations were collected in Gifu Prefecture, which is centrally located in Japan, during the season authorized to capture the animals; namely from December to March. Animals shot in their habitats were transported to Gifu University for examination, which is situated at 50 to 150 km distance from the sites of capture. The animals had been dead usually for a few days, sometimes for a week or more. Most materials were obtained exclusively from the bodies within 7 days after death. Some fresh materials were acquired at the site of capture within a few hours after the animal's death.

Table 1. **Examination items and number of animals**

Examination items	Transported materials			Fresh materials	
	Dec. 1982 untill Mar. 1983	Dec. 1983 untill Mar. 1984	Dec. 1984 untill Mar. 1985	Dec. 1982 untill Mar. 1983	Dec. 1983 untill Mar. 1984
Testis size	150	170	181		
Seminiferous tubule diameter	31			6	7
Population of primary spermatocytes				6	7
Testosterone concentration in testes		82	123		
Testosterone concentration in serum			107		5
Androstenedione concentration in testes			126		
Androstenedione concentration in serum			109		
Fructose concentration in seminal vesicle	71	93	10		
Body weight	166	182	197	6	7
Actual number of animals examined	166	182	197	6	7

Classification of age groups. The age estimation that underlies this study was based on the tooth eruption-wear patterns (Sugimura et al. 1981). The animals were classified into 6 age groups (Tab. 2). Animals of groups 0 to 2-I° are immature ones, in which the second dentition is not completed, and those of groups 2-I·II to 2-IV·V are adults in which all teeth are permanent.

Size of testis. The product of three dimensions of each testis was obtained, and the products for paired testes were summed.

Spermatogenic activity. The seminiferous tubule diameter was measured in one to three animals per month for every group; thus, in 15 youngs and 16 adults. The mean diameter was calculated from measurements of 10 cross sections of seminiferous tubules for each individual. Further, the number of primary spermatocytes at the pachytene stage per cross section of seminiferous tubule was counted using the fresh testicular materials removed from 13 animals (one to three animals per month in every age group except for 2-IV·V) at the sites of capture within a few hours after the animal's death. The mean number was calculated from measurements of 10 cross sections for each individual.

Testosterone and androstenedione in testicu-

Table 2. **Classification of age groups in Japanese serows**

Age group		Age in months or years
0		7–10 months
1		19–22 months
2-I°		31–34 months
2-I, 2-II	2-I·II	4.6 ± 1.8 years[1]
2-III		7.4 ± 2.7 years[1]
2-IV, 2-V	2-IV·V	12.7 ± 3.9 years[1]

[1] Calculated from the data on the patterns of cementum annulation in the teeth, which were presented by the courtesy of Dr. S. Miura

lar tissue. The testes without any pathological changes were used in this assay. Concentrations of testosterone and androstenedione were measured by radioimmunoassay using procedures similar to those described by Shodono et al. (1975) for the determination of estradiol and progesterone in the plasma. One gram of testicular tissue was homogenized and extracted in four steps with two volumes of ether. The extract was evaporated to dryness in N_2 gas stream, re-dissolved in 1 ml of ethanol and stored at −25 °C. Before use, 0.1 ml of the stored extract was evaporated and re-dissolved in BSA-PBS to 1 : 300 and 1 : 3 for testosterone and androstenedione assay, respectively.

[1, 2, 6, 7, 16, 17-^{3}H]-testosterone (138 Ci/mmol) and [1, 2, 6, 7 ^{3}H]-androstenedione (85 Ci/mmol) were used as competitors. Each of them was added to each test assay tube as 0.1 ml solution (8,000 cpm) in BSA-PBS. The anti-testosterone-11α-succinate-BSA serum and the anti-androstenedione-3-Oxime-BSA serum each were diluted with NRS-EDTA-PBS to 1 : 6,000. Cross reactivity of the anti-testosterone serum with androstenedione was 2.24 %, and that of the anti-androstenedione with testosterone 5.43 %.

One-fifth ml of testicular extract, 0.2 ml of antiserum and 0.1 ml of tritiated steroid were mixed. After incubation overnight at 4 °C, the steroids, unlabeled and labeled with tritium, were reacted with dextran-charcoal. Following centrifugation at 2,500 g for 15 min, 0.8 ml of the supernatant was removed. Eleven ml of toluene scintillator containing 0.4 % PPO and 0.01 % POPOP was added, and the radioactivity was measured with a liquid scintillation spectrometer. Unknown levels of steroids were read from a standard curve and expressed as nanograms per gram of testicular tissue.

In order to investigate the possibility of a lower testicular testosterone level during the period between the animal's death and tissue sampling, a comparison was made between the materials obtained, respectively, one to two days and 4 to 5 days after the animal's death. There was no significant difference between the former (444.19 ± 96.14 ng/g; n=8, adults, Dec.) and the latter (455.27 ± 60.01 ng/g; n=8; adults, Dec.).

Testosterone and androstenedione in serum. Serum samples were obtained from the coagulated blood in the heart and stored frozen at −25 °C. Concentrations of the steroids were measured with the same method as described above. After thawing the frozen samples, 0.6 ml of serum was extracted in three steps with four volumes of ether. The extract was evaporated to dryness in N_2 gas stream and re-dissolved in 0.6 ml ethanol. Before use, 0.05 ml of the extract was decanted into another test for testosterone assay, evaporated to dryness, and diluted with 0.2 ml BSA-PBS. For androstenedione assay, 0.2 ml of the extract was treated similarly. Further procedures were the same as described for the steroids in testicular tissue. Concentrations of the steroids were expressed as nanograms per milliliter serum.

In order to examine the possibility of a lower testosterone level during the period between the animal's death and serum sampling, a comparison was made between the transported and the fresh materials (see Tab. 1). There was no significant difference between the former (3.17 ± 0.26 ng/g; n=5, adults, Jan.~Mar.) and the latter (2.94 ± 0.44 ng/g, n=5; adults, Jan.~Mar.).

Fructose concentration in seminal vesicle: After obtaining the wet weight, the seminal vesicles were stored frozen at −25 °C. But owing to the tiny size of this organ in young animals, it was extremely difficult to acquire the minimum volume of material necessary for this chemical assay. Therefore, the seminal vesicles from animals of age groups 0 and 1 were pooled so as to provide enough material. After thawing of the frozen materials, the fructose contents were measured by the method of Lindner and Mann (1960).

To deal with the possibility of a lower fructose content during the period from the animal's death and seminal vesicle sampling, a comparison was made between the materials obtained, respectively, one and 4 days after the animal's death. There was no significant difference between the former (1.27 ± 0.43 mg/g; n=5; adults, Dec.) and the latter (1.04 ± 0.15 mg/g; n=5; adults, Dec.).

Apart from this assay, another experiment was carried out on the influence of storage upon fructose content using a bull's seminal vesicle. It was proved that the concentration remained unchanged at 4 °C for 7 days.

Body weight. As a supplementary method for determining the end of sexual maturation, the body weight was obtained in 545 animals for three consecutive seasons.

Results and statistical analysis. The mean values obtained have been shown with their standard error. Statistical comparisons between the mean values were made using Student's t test.

Results

Size of testis

The means and standard errors shown in Fig. 1 were calculated from measurement covering three consecutive capturing seasons. But before these mean values were obtained, the significance of difference in mean value between each single season was examined. No

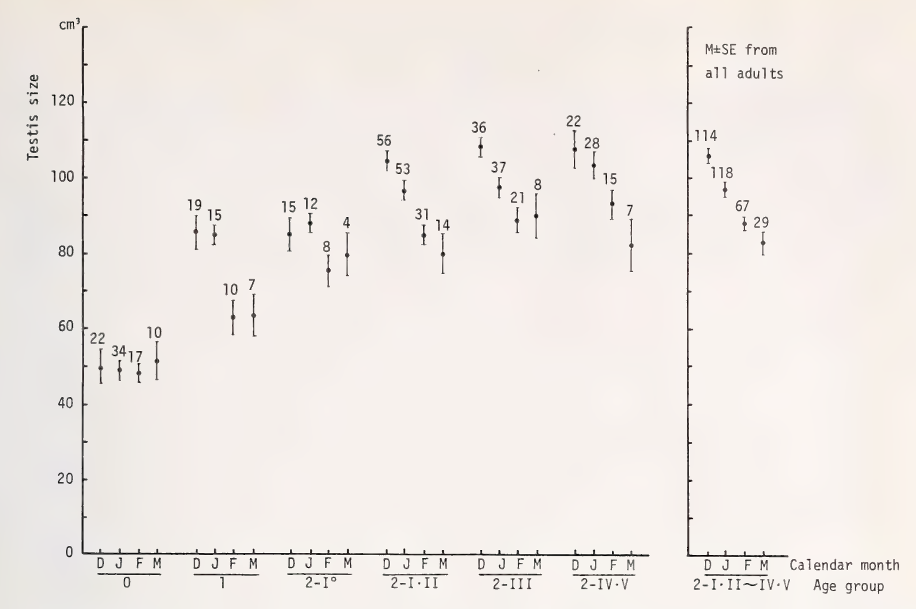


Fig. 1. Seasonal changes in combined size of paired testes for each age group of Japanese serows (M±SE, Dec. 1982–Mar. 1985). D: December; J: January; F: February; M: March. Numbers above bars represent sample size. In the following the same abbreviations are used

significant difference was found among the three seasons, and there was also no significant difference in size between paired testes.

As seen clearly in the figure, the testes grow rapidly between the age groups 0 and 2-I°, that is, from 7 months to about 2.5 years of age. The testes continue to grow slowly in the age groups 2-I·II, and thereafter the testis size is on a relatively constant level. In adults, a decrease in size occurs every year from December to March. Mean values taken from all the adults belonging to groups 2-I·II to 2-IV·V show a highly significant difference between two consecutive months ($p < 0.01$).

Testosterone concentration in testicular tissue

The first appearance of testicular testosterone is demonstrable in fawns at 7 to 10 months of age (Fig. 2). The concentration rapidly increases in age groups 0 to 2-I·II. In adults, the concentration varies widely. It is noticeable that, in age group 2-I·II, a significant increase is recognized between January and March (+196.9 %, $p < 0.05$%). A tendency to increase in the same month is found more or less in other groups except for age group 2-IV·V. But the mean value obtained from all the adults for December is significantly higher than in any other month ($p < 0.01$), and the increase from January to March is not significant.

Testosterone concentration in serum

An increase with age in the immature group is uncertain, but seasonal changes in the adults are relatively clear (Fig. 3). The mean value from all the adults in December is significantly higher than in any other months ($p < 0.01$). No significant difference was found among January, February and March.

It was also statistically clarified that there is a highly significant correlation between the concentration in serum and that in testicular tissue ($r = 0.814$, $p < 0.01$, $n = 112$).

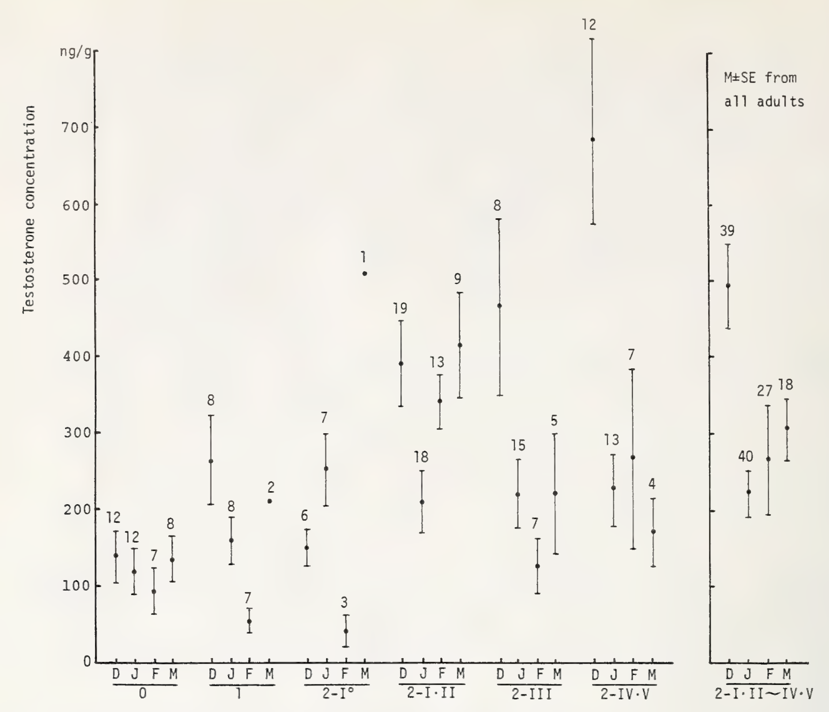


Fig. 2. Seasonal changes in testosterone concentration in testicular tissue for each age group of Japanese serows (M±SE, Dec. 1983–Mar. 1985)

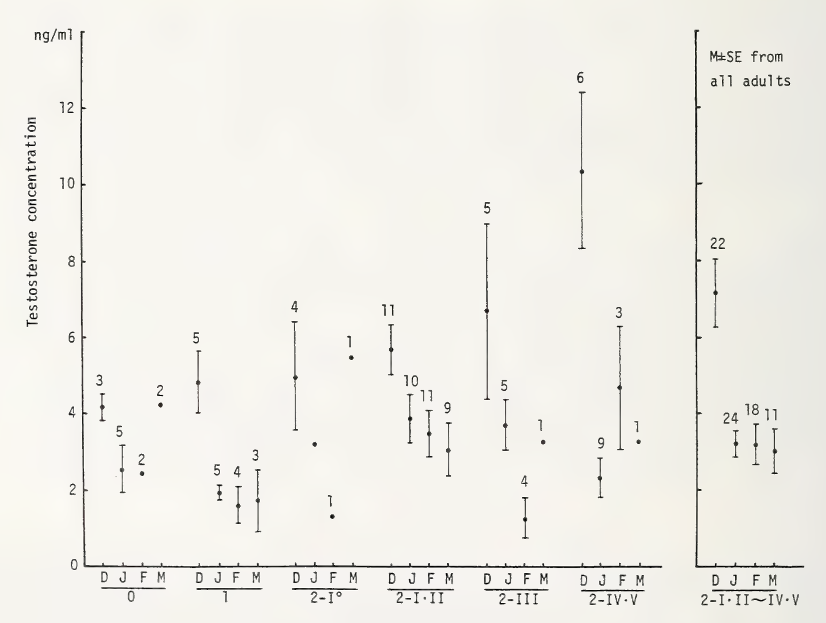


Fig. 3. Seasonal changes in testosterone concentration in serum for each age group of Japanese serows (M±SE, Dec. 1983–Mar. 1985)

Correlation between spermatogenic activity and testosterone level in testicular tissue

With the same animals in which both the seminiferous tubule diameter and the testosterone concentration in testicular tissue were measured, a correlation between the two was statistically analyzed. A highly significant correlation-coefficient was found (Fig. 4). On the other hand, in the fresh testicular materials obtained shortly after the animal's death, a highly significant correlation was found between the mean diameter of the seminiferous tubule and the mean number of the primary spermatocytes at the pachytene stage per cross section of the tubule (Fig. 5).

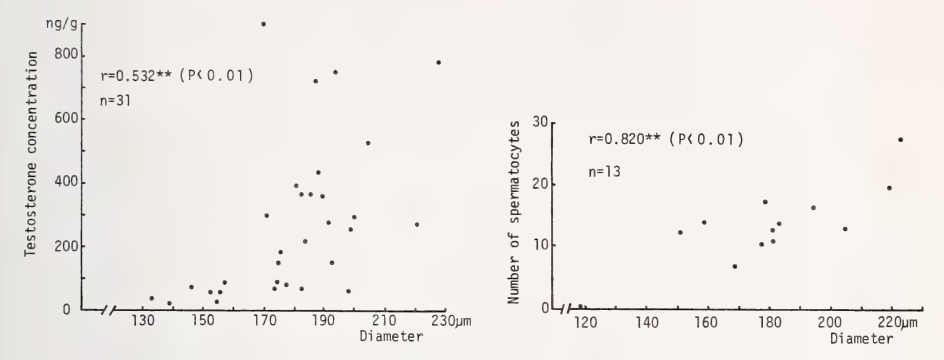


Fig. 4 (left). Correlation between seminiferous tubule diameter and testosterone concentration in testicular tissue of Japanese serows. – *Fig. 5 (right).* Correlation between seminiferous tubule diameter and number of pachytene primary spermatocytes per cross section of seminiferous tubule in Japanese serows

Androstenedione concentration in testicular tissue

In more than half of all animals examined (66/126), the androstenedione levels were under the lowest detection limit of the assay (45 pg/g). For this reason, no mean values were calculated, and the measured values were plotted for each individual in Fig. 6.

Androstenedione concentration in serum

As shown in Fig. 7, it is very difficult to find a decided tendency in the fluctuation of mean values for each age group. In the mean values calculated from all adults, the value for December is highest, showing a highly significant difference from that for February ($p < 0.01$). The second highest value in March shows a significant increase over February ($p < 0.05$), but is not significantly different from that in December.

Fructose concentration in seminal vesicle

The concentration of fructose per gram of seminal vesicle was determined (Fig. 8). For the reasons which have been advanced, however, no sufficient data for statistical analyses were obtained in the immature group, but the values obtained from young animals seem to be on a lower level than in adults. A decrease from December to March is statistically significant ($p < 0.01$) in the mean values calculated from all adults.

A statistical analysis of the correlation between fructose concentration in seminal vesicle and testosterone concentration in serum was conducted with the same animals in which both substances were evaluated. A highly significant correlation-coefficient was found between the two ($r = 0.75$; $p < 0.001$; $n = 38$).

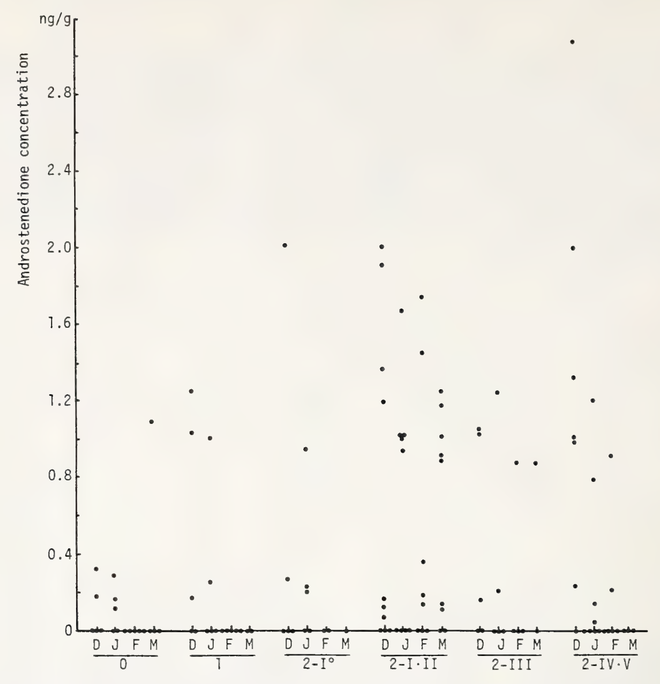


Fig. 6. Seasonal changes in androstenedione concentration in testicular tissue for each age group of Japanese serows. Spots on the abscissa indicate values below the lowest limit (45 pg/g)

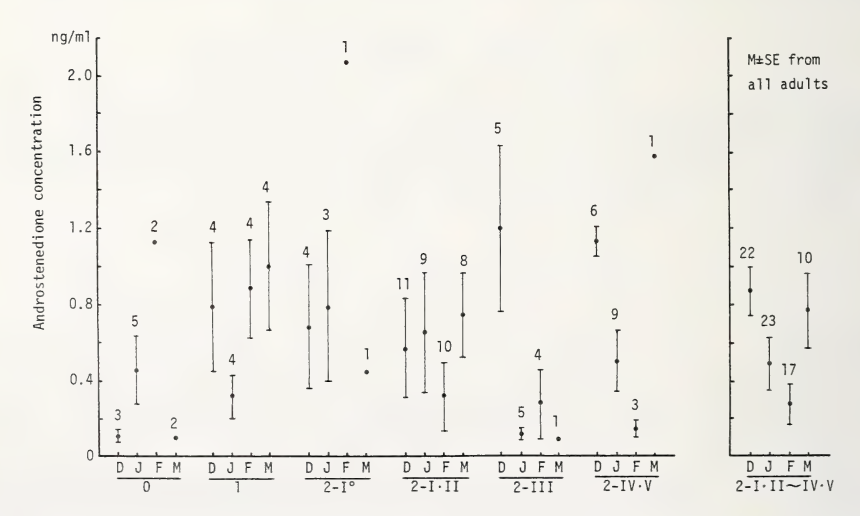


Fig. 7. Seasonal changes in androstenedione concentration in serum for each age group of Japanese serows (M±SE)

Body weight

It is clear from Fig. 9 that the growth of male animals ends at about 2.5 or 3 years of age, and thereafter the body weight is maintained on a relatively constant level. At a glance, the body weight appears to decrease steadily from December to March. However, the difference between the highest and the lowest values in each age group is not everywhere significant; thus, it is significant in group 1 (December to February: −19%; $p<0.01$), group 2-I·II (December to March: −9.4%; $p<0.01$) and group 2-III (December to February: −9.9%; $p=0.01$), but not in the other groups.

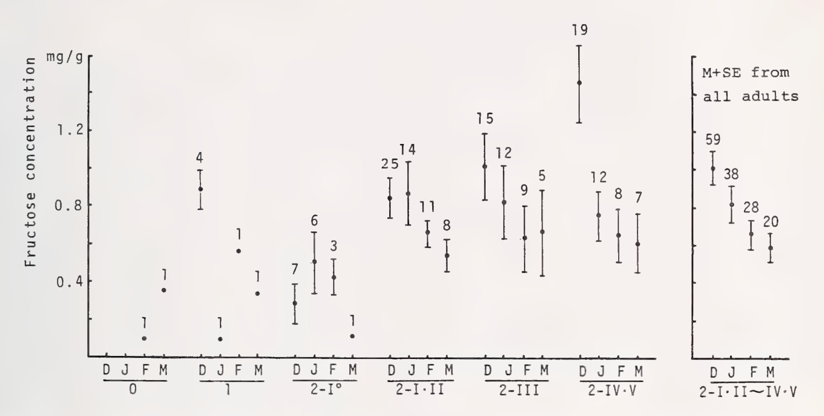


Fig. 8. Seasonal changes in fructose concentration in seminal vesicle for each age group of Japanese serows (M±SE, Dec. 1982–Mar. 1985). The values for age groups 0 and 1 were obtained from pooled material, except for the mean value for age group I in December (see text)

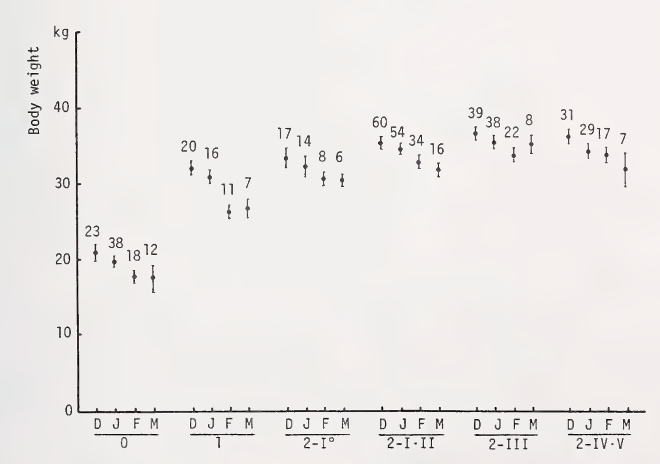


Fig. 9. Seasonal changes in body weight for each age group of Japanese serows (M±SE, Dec. 1982–Mar. 1985)

Discussion

From experiments in vitro about the metabolic routes of steroid hormone biosynthesis in the Japanese serow's testis (Nakamura and Suzuki 1985), it has been clarified that the ultimate product of androgen synthesis is testosterone in this species, too. And the major metabolic route in the testicular formation of testosterone from pregnenolone is Δ^5-pathway. It has also been demonstrated that androstenedione is produced only at a very low rate via the other minor metabolic route, Δ^4-pathway. These facts coincide with our own findings that androstenedione levels in testicular tissue as well as in serum are very low. It, therefore, can hardly be imagined that androstenedione plays an important role in the male reproductive functions of this animal. This supposition seems to be supported by our results that it was almost impossibile to find a relationship between the fluctuation in adrostenedione levels and advancing age or season.

In the goat, the domestic ruminant related most closely to the Japanese serow, the end-products in testicular formation of androgens from pregnenolone are testosterone and 17α, 20α-dihydroxy-4-pregnen-3-one; and testosterone is synthesized through both Δ^4- and Δ^5-pathways (Mori et al. 1980). As for the androstenedione levels in domestic ruminants, it is well known in the bull that the ratio androstenedione/testosterone decreases with age (Lindner and Mann 1960). Concerning changes in adrostenedione levels with advancing age in the young goat, there is a discrepancy in the literature. Leidl et al. (1970) reported, in measuring testicular androgens that there was no change in the ratio androstenedione/ testosterone. On the contrary, Saumande and Rouger (1972) mentioned from the result of determination of the plasma testosterone level in one young goat of Saanen breed, that during the period of lower testicular activity androstenedione is more important than testosterone. In the ram, the testicular concentration of testosterone is always higher than that of androstenedione between the 5th and 12th month of life (Eik-Nes 1975). The sexual maturation in this animal occurs just in this period (Hulet and Shelton 1980).

Our previous indication that the testicular functions in Japanese serows are subject to seasonal fluctuation (Tiba et al. 1981a), is now clearly demonstrated by the findings that the testosterone levels in the testicular tissue as well as in serum are significantly higher in December than in any other months. It has been also clearly demonstrated in this study that the fructose content in the seminal vesicle is seasonally changeable, depending upon the testosterone level. However, we do not yet know all about the seasonal fluctuations in this animal's reproduction. The height of the breeding season is, as mentioned before, October and November, when the concentrations of steroids and fructose must be placed on even higher levels than in December.

On the contrary, the spermatogenic activity in the goat does not fluctuate in parallel with the testosterone levels in testicular tissue (Leidl et al. 1970). According to these authors, "The seasonal rhythm of reproduction in the male goat affects only the functional relationship 'androgens-accessory sexual glands-seminal plasma and contents', whereas the germinal cells show no fluctuations." And the authors add: "These findings suggest that spermatogenesis continues to be stimulated by amounts of hormones which are insufficient to stimulate the accessory sexual glands to their full function."

It is clear from the results that the sexual maturation in this animal is completed at 2.5 to 3 years of age. This coincides with the report mentioned earlier that the first parturition in female occurred usually at 3 years of age. In our own studies on morphology of ovaries and fetuses, female serows become sexually mature at about 2.5 years of age. The youngest pregnant females were 30 months old (Kita et al. 1983). If male Japanese serows reach puberty within 6 or 7 months after birth and come to full sexual maturation at 2.5 to 3 years of age, there is an interval of 2 to 2.5 years between the beginning and the end of sexual maturation. This interval appears extremely long as compared with domestic

ruminants. Bulls (HAWK and BELLOWS 1980), rams and goats (HULET and SHELTON 1980) are brought into service either via natural or artificial insemination after an interval of a few to 6 months, or at most one year following puberty. Such a comparison, however, may not be reasonable, because in domestic animals the sexual maturation is hastened by a high level of nutrition, artificial selection and other beneficial conditions. In wild ruminants, we were not able to find any reports in which the beginning and the end of sexual maturation are separately described.

Acknowledgement

The authors wish to thank Dr. T. NAKAMURA for providing informations on RIAs.

Zusammenfassung

Jahresrhythmische Veränderungen von Fortpflanzungstätigkeiten und Geschlechtsreife beim männlichen Japanischen Serau (Capricornis crispus)

Die Fortpflanzungstätigkeit wurde bei zahlreichen männlichen Exemplaren des Japanischen Serau untersucht, die 1982–1985, von Dezember bis März, in der Provinz Gifu in Zentraljapan erlegt wurden. Die Prüfungen erstreckten sich auf spermatogenetische Tätigkeit, Testosteron- und Androstendionkonzentration im Hodengewebe sowie im Serum und auf Fruktosekonzentration in der Samenblase. Bei vollwüchsigen Männchen über 2,5 bis 3 Jahre wurde der Maximalwert bei jeder Prüfung fast ausnahmslos im Dezember gewonnen. Von Dezember bis in den März hinein, zeigte sich eine offensichtliche Tendenz zur Herabsetzung der Werte. Eine hochsignifikante Korrelation wurde festgestellt, sowohl zwischen der spermatogenetischen Tätigkeit und der Testosteronkonzentration, als auch zwischen der Fruktosekonzentration und dem Testosteronspiegel. Daraus geht schon hervor, daß die männlichen Fortpflanzungstätigkeiten dieser Spezies den jahreszeitlichen Schwankungen unterworfen sind. Bei jungen Tieren steigerten sich die spermatogenetische Aktivität und die Testosteron- sowie Fruktosekonzentration mit zunehmendem Alter und erlangten das Niveau des Erwachsenen im Alter von 2,5~3 Jahren. Die Androstendionkonzentration im Serum bei Jungen steht auf gleicher Höhe mit der von Erwachsenen, und es gab keine deutliche Tendenz zur Herabsetzung der Werte im Laufe der sexuellen Reifung.

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Z. Säugetierkunde 53 (1988) 189–190

ISSN 0044-3468

WISSENSCHAFTLICHE KURZMITTEILUNG

An unusual record of Hooded seal *(Cystophora cristata)* in SW Spain

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Receipt of Ms. 3. 8. 1987

The Hooded seal, *Cystophora cristata,* is a typical Arctic species from the central and western areas of the northern Atlantic. Its distribution extend from Newfoundland and Labrador to Greenland, Iceland, Bear Island and Spitsbergen (Reeves and Ling 1981; Kovacs and Lavigne 1986). In very rare occasions, wandering solitary individuals have been reported on both sides of the Atlantic as far south as Florida (USA) and Portugal (King 1983).

On February 26, 1983, a specimen of Hooded seal was found dead on the beach near Torre Zalabar in Doñana National Park, 10 km NW of the mouth of the Guadalquivir river in the Province of Huelva, Spain (36° 54′N, 6° 24′W). The specimen was a pregnant adult female and showed a deep wound, measuring approximately 20 cm, on its right side. The death was recent as the animal was well preserved except for the eyes which had been eaten. The skin, the skeleton and the foetus are deposited in the collection of the Estación Biológica de Doñana (CSIC, Sevilla).

External and cranial measurements (in millimeters), the latter taken according to Wiig and Lie (1984), and the weight (in kilograms) of the specimen were as follows: total length (nose-tail), 2010; tail length (from anus), 155; posterior extremity length (with cartilage), 350; anterior extremity length, 303; condylobasal length, 2411; basal length, 225; palatal length, 134; upper tooth-row length, 78; zygomatic width, 185; auditory meatus width, 157; palatal width, 60; orbital width, 33; mandible length, 158; weight (with foetus), 116. Except for the weight, which was greatly inferior to that considered normal for an adult female (Reeves and Ling 1981; Kovacs and Lavigne 1986), these measurements are among the highest reported for the species, corresponding to an age well over 20 years (Wiig 1985). The total length of the foetus was 75 and the weight 9.5.

The nearest localities to Doñana where the species has been reported are two in France (I. Oléron, in Charente-Maritime, and Bidasoa) (Pouvreau et al. 1980) and three in Portugal (Buarcos, Algarve and Peniche) (Reiner 1979, 1980). All these cases dealt with young individuals, observed between June and August. Although the reports from Bidasoa and Algarve are close to the Spanish coast, this is the first concrete record for Spain and the furthest from the habitual range of the species. The importance of this new record, however, lies in the fact that it deals with an adult individual, as opposed to the others in these latitudes which were undoubtedly related to juvenile dispersion.

Although of advanced age, this specimen cannot be considered senile, as it presented normal reproductive activity. At the time of death, it was in poor physical condition. The subcutaneous layer of fat, which reaches a tickness of 4.8 cm at this time of year (Reeves and Ling 1981), was reduced to 1 cm and the specimens's weight was, as previously mentioned, well below normal. The evidence would indicate the seal died after depleting

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its reserves, perhaps as a result of the wound in its side which made it incapable of obtaining food. The decrease in its faculties probably led to its being swept by the ocean streams to the Spanish coast.

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NAUTA, W. J. H.; FEIRTAG, M.: **Fundamental neuroanatomy.** New York: Freeman and Co. 1986. 340 pp., 116 figs. £ 18.95. ISBN 0-7167-1723-9

In diesem Buch geben die bekannten Autoren einen Überblick über den Grundbauplan des Säugetiergehirns, vornehmlich am Beispiel des Menschen. Sie haben die Stoffülle in drei große Abschnitte unterteilt und gehen in üblicher Weise synthetisch vor. Im einleitenden Kapitel wird sehr kurz auf frühe stammesgeschichtliche Entstehung nervöser Strukturen und auf die Situation bei basalen Evertebraten eingegangen. Es folgt eine Beschreibung von Neuronen und Gliazellen in Bau und Funktion (Darstellungsmethoden, Möglichkeiten von Neuronenkontakten, Mechanismen der Reizleitung, Transmittersubstanzen etc.). In einer Übersicht werden dann die großen Hirnteile in ihrer Ontogenese und adulten Organisation skizziert sowie Prinzipien retrograder und anterograder Degenerationstechnik. Ein zweiter Abschnitt ist den Verbindungen und Funktionssystemen im Gehirn gewidmet, indem auf die großen afferenten und efferenten Systeme, auf neocorticale Funktionen, viscerale Innervation und limbisches System eingegangen wird. Der dritte Abschnitt schildert die anatomischen Verhältnisse. An Hand von Querschnittspräparaten und Zeichnungen werden in Form eines Hirnatlas Kerngebiete und Faserzüge der verschiedenen Hirnteile des Menschen benannt und besprochen.

Das Buch ist in klarer Sprache abgefaßt und verständlich geschrieben. Die wichtigsten Fortschritte in der Geschichte der Hirnforschung sowie Erklärungen und Ableitungen sehr vieler wissenschaftlicher Namen sind geschickt in den Text eingeflochten. Die Bebilderung mit Originalpräparaten von außerordentlicher Qualität, Blockdiagrammen und Schaltschemata beeindruckt und gewinnt zusätzlich an Wert durch besonders ausführliche, erläuternde Unterschriften. Insgesamt liegt eine gelungene und kurzgefaßte Informationsquelle über dieses Organ vor, die jeden Interessenten ansprechen muß.

D. KRUSKA, Kiel

HILDEBRAND, M.; BRAMBLE, D. M.; LIEM, K. E.; WAKE, D. B. (eds.): **Functional Vertebrate Morphology.** Cambridge Mass., London: The Belknap Press of Harvard University Press 1985. 430 pp. US $ 40.25. ISBN 0-674-32775-6

Die langwährende Stagnation der vergleichenden Morphologie ist heute weitgehend überwunden. Sie beruhte letzten Endes auf der Reduktion der Formenkunde auf einen geschlossenen, typologischen Formbegriff. Die Einsicht in den essentiellen Zusammenhang und die Untrennbarkeit von Form und Funktion in der Organismenwelt führte in den vergangenen zwei Jahrzehnten zur Überwindung der Erstarrung und zu neuen Denkweisen. Diese sind gekennzeichnet durch die Einbeziehung experimenteller und quantitativer Methoden, durch Berücksichtigung von Lebensweise, Verhalten und Umwelt, durch Einführung neuer technischer Verfahren (z.B. Bewegungsanalyse durch Elektromyographie und vieles andere). Umwelt und Organismus sind historischen Einflüssen unterworfen. Daher bleibt die Beachtung des zeitlichen Faktors (Evolutionsbiologie), der schon früher eng mit der Morphologie verknüpft war, eine notwendige Voraussetzung. Schließlich vermag die Analyse des individuellen Zyklus (Embryologie) grundsätzliche Einsichten zu vermitteln. Das vorliegende Buch ist ein hervorragendes Beispiel für den Wandel in Denk- und Arbeitsweisen der vergleichenden Morphologie heute.

Das von 20 Autoren bearbeitete Werk setzt Grundkenntnisse der Anatomie, Physiologie und Formenkunde voraus, ist also nicht für den Anfänger geeignet. In zwei einleitenden Kapiteln werden funktionelle Anpassung bei Skelettstrukturen (leider ohne Berücksichtigung der Arbeiten von PAUWELS und KUMMER) und Probleme der Körpergröße und Allometrie behandelt. Das Kernstück des Werkes sind die sieben Beiträge über verschiedene Lokomotionsweisen (Laufen, Springen, Klettern, subterrane Lokomotion, Schwimmen, Fliegen, Bewegung ohne Gliedmaßen). Es folgt je ein Beitrag über Energetik der Lokomotion und Atmung. Drei Kapitel befassen sich mit Biologie der Nahrungsaufnahme – Kauakt. Zwei Beiträge sind den Sinnessystemen (Octavo-Lateralis und Auge) gewidmet. Die zentralnervöse Kontrolle und Koordination wird in einem inhaltsreichen Kapitel berücksichtigt. WAKE und LIEM fassen in einem Schlußbeitrag „Morphology, current approaches and concepts" die derzeitige Situation in einer Synthese zusammen. Skelett und Lokomotion stehen ganz im Vordergrund der Darstellung (nahezu die Hälfte des Inhaltes). Ursache hierfür ist natürlich die Tatsache, daß Skelett und Lokomotion am leichtesten der morphologischen und physikalisch-technischen Untersuchung zugänglich sind.

Die Ausstattung des Buches ist hervorragend. Hervorgehoben sei, daß die verschiedenen Beiträge inhaltlich und stilistisch außerordentlich gut aufeinander abgestimmt sind und sich so – im Gegensatz zu manchen Büchern mit vielen Autoren – ein geschlossenes Ganzes ergibt. Ihm ist weite Verbreitung zu wünschen, zumal es neue Denkweisen und Methoden in einer verjüngten Wissenschaft dokumentiert.

D. STARCK, Frankfurt/M.

KREBS, J. R.; DAVIES, N. B: **An Introduction to Behavioural Ecology.** 2. Ed. Oxford: Blackwell Scientific Publications 1986. 400 pp., 121 ill., £ 12.80. ISBN 0-632-01498-9

Die erste Auflage der „Einführung . . ." in dieses moderne Gebiet der Ethologie war sowohl in der englischen als auch in der deutschen Ausgabe ein Erfolg. Es ist die augenblicklich einzige auf dem Markt zu erhaltende Einführung in die Verhaltensökologie. So ist es zu begrüßen, daß eine 2. Aufl., die um ca. 100 S. erweitert und an zahlreichen Stellen ergänzt wurde, erschienen ist. Fast alle Kapitel wurden wenigstens zum Teil neu verfaßt, und es sind neue Schwerpunkte hinzugekommen, wie z. B. die Kapitel über „Konkurrenz und Ressourcen" und über „Selbstsucht und Altruismus". Erweitert wurden die Kapitel „Kämpfen und Einschätzen" sowie über „elterliche Fürsorge und Paarungssysteme". Das Literaturverzeichnis, das um 8 S. verlängert wurde, spiegelt den Stand der augenblicklichen einschlägigen Literatur gelungen wider. R. SCHRÖPFER, Osnabrück

SAVAGE, R. J. G.; LONG, M. R.: **Mammal evolution: an illustrated guide.** London: British Museum (Nat. Hist.) 1986. 259 pp. £ 17.50. ISBN 0-565-00942-7

In this book, the British palaeontologist R. J. G. SAVAGE gives a short overall description of the modern knowledge on mammalian phylogeny. The subject-matter is presented in 13 chapters starting with general informations on the geology of fossilisation and natural preservation processes, continental drift during earlier times, dating methods and geological times. Then, a characterisation of mammals and a higher classification of this animal group is given. Furtheron, bones and teeth as well as other anatomical peculiarities of different adaptive forms are outlined and characteristics to differentiate reptiles and mammals. Mammal like reptiles and early mammals are sketched. The descriptions on ancient and recent mammals as well as their distribution, phylogenetical development and evolution are done in nine further chapters headlined as: insectivores, carnivores, paddlers and swimmers, gliders and fliers, gnawers, early rooters and browsers, mammals on island and continents, hoofed herbivores, and men and monkeys. Consequently, the author preferred a summarized description in connection with special adaptations and life-style types. In connection with and additional to the text there is a considerable amount of illustrations done by the junior author M. R. LONG. These illustrations are high quality drawings of species' habits as well as anatomical details (bones, teeth, skulls, intestines, endocasts, etc.). Very impressive coloured restorations of ancient forms in ancient landscapes are especially welcome to the reader because of their imaginative value. The book can be recommended not only to mammalogists but also to persons with general interests as a source of overall information. D. KRUSKA, Kiel

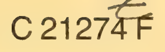
SCHEUNERT, A.; TRAUTMANN, A.: **Lehrbuch der Veterinär-Physiologie.** 7., völlig neubearb. Aufl., hrsg. von G. WITTKE. Berlin und Hamburg: Paul Parey 1987. 739 S., 418 Abb., 116 Tab. DM 198,–. ISBN 3-489-66216-4

Dieses Lehrbuch der Veterinär-Physiologie nimmt seit der 1. Aufl., von SCHEUNERT, TRAUTMANN, KRZYWANEK 1939 begründet, einen festen Platz in der Ausbildung der Tiermediziner ein. Ausgewiesene Wissenschaftler waren auch in der Folge an den Gestaltungen weiterer Auflagen beteiligt, die 6. war bereits 1982 nicht mehr erhältlich. Nun liegt, bedauerlicherweise verzögert, die 7., von G. WITTKE herausgegebene Auflage vor. Die Bearbeitung der verschiedenen Kapitel teilen sich 16 Wissenschaftler in folgender Konzeption: Allgemeine Grundlagen der Lebensvorgänge (EDER/WITTKE/WELS), Stoff- und Energiewechsel (SCHARRER/PFEFFER/GROPP/MÄNNER/BRONSCH/ZUKKER), Thermophysiologie (HÖRNICKE), Blut und Lymphe (EDER), Blutkreislauf (SPÖRRI), Atmung (SPÖRRI/WITTKE), Wasser- und Elektrolythaushalt, Physiologie der Niere (HIERZOLZER/FROMM), Endokrinium (BAMBERG), Fortpflanzung (ZEROBIN), Eibildung (MÄNNER), Nervensystem und Sinnesorgane (WITTKE), Bewegung (WELS), Verhalten (HOFECKER). Gegenüber der vorangegangenen Auflage sind mehrere Abschnitte revidiert, erweitert und modernisiert, andere neu aufgenommen worden. Auf Darstellung biochemischer Prozesse wurde wegen der Ausgliederung dieses heute eigenständigen Faches und entsprechender Ausstattung mit eigenen Lehrbüchern verzichtet. Den Erfordernissen einer einsichtigen Haustierhaltung entsprechend, wurde auch die Verhaltensphysiologie neu bearbeitet. Die Ausführungen sind kurz und prägnant, und im Hinblick auf die zahlreichen Autoren zeigt der Text eine erwähnenswerte, flüssige Einheitlichkeit. Obwohl in erster Linie an klinisch-medizinischer Anwendung orientiert, enthält dieses Lehrbuch sehr viel Information, so daß es auch Säugetierkundlern allgemein empfohlen werden kann. D. KRUSKA, Kiel

Erscheinungsweise und Bezugspreis 1988: 6 Hefte bilden einen Band. Jahresabonnement Inland: 308,– DM zuzüglich 13,80 DM Versandkosten, Gesamtpreis 321,80 DM einschließlich 7 % Mehrwertsteuer. Jahresabonnement Ausland: 308,– DM zuzüglich 18,– DM Versandkosten. Das Abonnement wird zum Jahresanfang berechnet und zur Zahlung fällig. Es verlängert sich stillschweigend, wenn nicht spätestens am 15. November eine Abbestellung im Verlag vorliegt. Die Zeitschrift kann bei jeder Buchhandlung oder bei der Verlagsbuchhandlung Paul Parey, Spitalerstraße 12, D-2000 Hamburg 1, bestellt werden. Die Mitglieder der „Deutschen Gesellschaft für Säugetierkunde“ erhalten die Zeitschrift unberechnet im Rahmen des Mitgliedsbeitrages.

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Vol. 53 (4), 193–256, August 1988 ISSN 0044-3468 C 21274 F



ZEITSCHRIFT FÜR SÄUGETIERKUNDE

INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Organ der Deutschen Gesellschaft für Säugetierkunde





Verlag Paul Parey Hamburg und Berlin

This journal is covered by Biosciences Information Service of Biological Abstracts, and by Current Contents (Series Agriculture, Biology, and Environmental Sciences) of Institute for Scientific Information

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Die Zeitschrift für Säugetierkunde veröffentlicht Originalarbeiten und wissenschaftliche Kurzmitteilungen aus dem Gesamtgebiet der Säugetierkunde, Besprechungen der wichtigsten internationalen Literatur sowie die Bekanntmachungen der Deutschen Gesellschaft für Säugetierkunde. Verantwortlicher Schriftleiter im Sinne des Hamburgischen Pressegesetzes ist Prof. Dr. Harald Schliemann.

Zusätzlich erscheint einmal im Jahr ein Heft mit den Abstracts der Vorträge, die auf der jeweiligen Hauptversammlung der Deutschen Gesellschaft für Säugetierkunde gehalten werden. Sie werden als Supplement dem betreffenden Jahrgang der Zeitschrift zugeordnet. Verantwortlich für ihren Inhalt sind ausschließlich die Autoren der Abstracts.

Manuskripte: Manuskriptsendungen sind zu richten an die Schriftleitung, z. Hd. Prof. Dr. Dieter Kruska, Institut für Haustierkunde, Biologie-Zentrum, Neue Universität, Olshausenstr. 40–60, D-2300 Kiel. Für die Publikation vorgesehene Manuskripte sollen gemäß den „Redaktionellen Richtlinien" abgefaßt werden. In ihnen finden sich weitere Hinweise zur Annahme von Manuskripten, Bedingungen für die Veröffentlichung und die Drucklegung, ferner Richtlinien für die Abfassung eines Abstracts und eine Korrekturzeichentabelle. Die Richtlinien sind auf Anfrage bei der Schriftleitung und dem Verlag erhältlich.

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Fortsetzung 3. Umschlagseite

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Z. Säugetierkunde 53 (1988) 193–201

ISSN 0044-3468



Lernversuche in einer Zweifachwahlapparatur zum Hell-Dunkel-Sehen des Maulwurfs (*Talpa europaea* L.)

Von Kristina Johannesson-Gross

Aus dem Fachbereich 19 (Biologie/Chemie) der Universität Kassel

Eingang des Ms. 15. 05. 1987

Abstract

Brightness discrimination of the mole (Talpa europaea L.) in learning experiments applying a modified tube-maze method

Studied was the light-dark discrimination of the mole *(Talpa europaea)* in learning experiments applying a special maze method. 8 animals (caught outside and tamed before the experiment) were trained to the light side of a modified tube-maze. The results were shown in quantity in learning curves. It became evident that moles can learn to distinguish between light and dark. 6 moles learned the task at a degree of illumination of 350 lux on the light (reinforced) side. 2 other animals reached the criterion level (90 % correct responses in 30 trials) not before an increase in illumination to 500 lux being the next phase of the experiment. The initially offered degree of illumination of 60 lux proved too low as a sign of discrimination. There were no temperature differences between the light and the dark side of the two-choice-training apparatus. And there was no indication whatever that moles find their way by means of infrared radiation. The possible role of the perception of light impulses from the mole in life conditions, especially the ecological function of the optical sense is discussed.

Einleitung

Talpa europaea lebt weitgehend unterirdisch in einem selbstgegrabenen und in großen Teilen dauerhaften Tunnelsystem (Godfrey und Crowcroft 1960; Quilliam 1966b; Mellanby 1974). Seine subterrane und fossoriale Lebensweise bedingt mannigfaltige anatomische und physiologische aber auch verhaltensmäßige Sonderanpassungen. So darf man bei ihm eine spezielle Lerndisposition zur Raumorientierung erwarten. Auf diesem Gebiet sind unsere Kenntnisse aber äußerst lückenhaft, systematische experimentelle Forschungen liegen kaum vor.

Von den bisher untersuchten Sinnessystemen des Maulwurfs (vgl. Quilliam 1966c, d) hat sich der Tastsinn als besonders hoch entwickelt erwiesen. Ihm wird eine große Bedeutung für das Zurechtfinden in den verzweigten dunklen Gängen beigemessen (u. a. Kriszat 1940a, b, c; Godet 1951; Quilliam und Armstrong 1963). Lernversuche zur taktilen Orientierung beim Wegelernen in Labyrinthen haben diese Auffassung experimentell bestätigt (Chrzanowski 1972; Johannesson-Gross 1984, 1986).

Im Gegensatz zum Tastsinn ist der Gesichtssinn der Talpidae in unterschiedlichem Ausmaß rückgebildet. Unter den Altweltmaulwürfen (zu den Verhältnissen bei den Scalopinae siehe Slonaker 1902; Lewis 1983) weist das Auge von *Talpa europaea* noch den geringsten Reduktionsgrad auf. Wie licht- und elektronenmikroskopische Untersuchungen erkennen lassen, besitzt es alle für ein Sehen notwendigen Strukturen, zeigt aber deutliche Abweichungen vom Bau eines typischen Säugetierauges (Ciaccio 1875; Kohl 1893, 1895; Rochon-Duvigneau 1943; Henderson 1952; Quilliam 1966a; Siemen 1976). Nicht immer ist das winzige Auge des Maulwurfs (∅ ca. 1 mm) sichtbar. Meistens liegt es von Haut überdeckt unter dem Fell verborgen. In manchen Situationen tritt es jedoch aus der Lidspalte heraus und kommt zum Vorschein (Abb. 1). Dieses Phänomen ist verschiedenen Autoren zwar aufgefallen (Scheffer 1949; Tusques 1954; u. a.), trotzdem

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Abb. 1. Maulwurf mit hervortretendem Auge beim Verlassen einer Röhre

wurde *Talpa europaea* aber weithin für ein blindes Tier gehalten (z.B. Suzuki und Kurosomi 1972; Pevet et al. 1981) oder zumindest für ein solches mit nur wenig ausgeprägtem optischen Leistungsvermögen (Mellanby 1982).

Erste verhaltensexperimentelle Ansätze zur Prüfung des Gesichtssinnes dieser Tierart finden sich bei Kriszat (1940a) sowie bei Lund und Lund (1965, 1966). Während Kriszat eine Dressur des Maulwurfs auf ein Lichtsignal nach der Methode der klassischen Konditionierung nicht gelang, konnten Lund und Lund (1965) durch operantes Konditionieren ein positives Ergebnis erzielen. Allerdings war der lediglich von 4 Tieren erreichte Lernerfolg ausgesprochen instabil, und große individuelle Schwankungen der Lerndauer traten auf. Da außerdem in den entsprechenden Publikationen keine Lernkurven vorgestellt wurden, war dies Anlaß, weiterführende Lernexperimente mit *Talpa europaea* zum Problemkreis des Hell-Dunkel-Sehens anzustellen und zu prüfen, ob und in welchem Ausmaß sich diese Tiere nach Helligkeitsdifferenzen räumlich orientieren können.

Material und Methode

Zur Untersuchung des optischen Leistungsvermögens wurde eine maulwurfsadäquate – im Hinblick auf die spezifische Fragestellung erweiterte – Röhrenlabyrinthmethode entwickelt, mit der es möglich war, durch Futterbelohnung positiv verstärkte Zweifachwahlen auf Hell (belohnt) gegen Dunkel (unbelohnt) durchzuführen. Zum Prinzip der Methode siehe Abb. 2 und Johannesson-Gross und Gross (1982).

Die Lernapparatur ist aus farblos-transparenten Kunststoffteilen zusammengesetzt. Sie besteht aus dem Entscheidungsraum (einem nach oben und unten offenen Plexiglaskasten) und aus insgesamt 3 PVC-Röhren. Eine dieser Röhren führt als Eingang in den Entscheidungskasten hinein. Ihr gegenüber liegt die Wahlseite der Apparatur mit 2 ebensolchen Röhren als Ausgängen (Abb. 3). Durch Überstülpen zweier Abdeckelemente kann eine der beiden Ausgangsröhren lichtundurchlässig gemacht werden. Die andere Ausgangsröhre bleibt hell und stellt so die Richtigwahlseite dar (Abb. 3b). Als zusätzliche visuelle Orientierungshilfe dienen 2 gegeneinander austauschbare Schieber. Sie sind zwischen Kastenaußenseite und Röhrenbeginn eingesetzt, jeweils fast die Hälfte der Seite einnehmend (Abb. 3a, b). Der eine Schieber ist mit weißer, der andere mit schwarzer d-c-fix-Folie beklebt. Darüber befindet sich zusätzlich ein Überzug aus gleichartiger durchsichtiger Schutzfolie.

Zu Beginn eines jeden Durchganges befindet sich das Versuchstier (VT) im Startelement (Abb. 3b). Wird dieses geöffnet, läuft das VT bis zum Entscheidungsraum vor und gelangt über eine 3 cm hohe Stufe in diesen hinein. Um von dort den Lauf in der dunklen (falsch) oder hellen (richtig) Röhre fortzusetzen, muß das VT noch einmal eine 3 cm hohe Stufe überwinden. Diese Stufen (wie der ganze Entscheidungskasten überhaupt) sollen durch Anhalten bzw. Verzögern des Laufes die Wahrscheinlichkeit des Beachtens visueller Reize durch die VT erhöhen. Erreicht der Maulwurf das Zielelement, wird es hinter ihm verschlossen, das Belohnungsloch geöffnet und eine Mehlkäferlarve als positive Verstärkung geboten. Ist diese gefressen, wechselt das VT in das Pausenelement über, von wo es vor Beginn des nächsten Durchganges erneut in das Startelement gelassen wird (Abb. 2).

Pro VT fanden täglich 10 Durchgänge nacheinander statt. Zum Ausschließen geruchlicher

Abb. 2. Schema zum Versuchsablauf. Abholen eines Maulwurfs vom Haltungskäfig und Transport zum Startelement der Versuchsapparatur (1, 2); insgesamt 10 Durchgänge (= Läufe) hintereinander werden von jedem Tier während einer Lernsitzung absolviert (3, 4); Rücktransport zur Käfiganlage (5). Zwischen den Haltungskäfigen und der Versuchsanlage besteht durch die Transport- und Pausenelemente ein räumliches Kontinuum, keines der Tiere muß während der Versuche angefaßt werden

Einflüsse wurden die Röhren nach jedem Durchgang mit reinem Alkohol ausgewischt, und die Fließpapierunterlage (Abb. 3b) wurde gewechselt. Neonröhren und 3 Zusatzlichter in Form von 100-Watt-Glühlampen (Abb. 3b) leuchteten die Wahlapparatur gleichmäßig aus. Durch Variieren des Abstandes von L 3 zur Anlage konnte die Beleuchtungsstärke der belohnten Seite und damit der Hell-Dunkel-Unterschied zwischen den beiden Ausgangsröhren eingestellt und schrittweise verändert werden. L 1 und L 2 blieben in ihrer Position unverändert. Die belohnte Seite der Zweifachwahlapparatur wurde für jeden Durchgang nach Zufall bestimmt, wobei aber dieselbe Seite höchstens an 2 aufeinanderfolgenden der insgesamt 10 Durchgänge die belohnte sein konnte. Temperaturunterschiede zwischen den beiden Wahlseiten waren nicht feststellbar (Sekunden-Thermometer mit Oberflächenmeßfühler Technotherm Typ 3000, Ablesegenauigkeit ± 1/10 °C). Als Lernparameter fand die prozentuale Häufigkeit der Richtigläufe (RL) in 10 Durchgängen Verwendung. Das Lernkriterium galt als erfüllt, sobald vom VT durchschnittlich 90 % RL an 3 aufeinanderfolgenden Tagen erreicht waren. Getestet wurden 8 Wildfänge der Art *Talpa europaea* verschiedenen Alters und Geschlechts, die zu Versuchsbeginn alle handzahm waren. Spontantendenzen der Seitenwahl waren nicht nachweisbar.

Ergebnisse

Entsprechend der schrittweisen Änderung der Beleuchtungsbedingungen auf der belohnten Wahlseite der Lernapparatur bestand die Dressur auf Hell-Dunkel-Unterschiede aus 3 Versuchsteilen.

Versuchsteil I: Die Beleuchtungsstärke auf der belohnten Seite betrug 60 Lux. Unter diesen Bedingungen bleibt die durchschnittliche prozentuale Häufigkeit der RL aller VT (T 1 bis T 6) vom 1. bis zum 60. Tag im Zufallsbereich (Abb. 4a). Bei keinem einzelnen der 6 Tiere war eine Bevorzugung der belohnten (hellen) Seite feststellbar.

Versuchsteil II: Die VT wurden in der gleichen Weise wie in dem unmittelbar vorausgegangenen Versuchsteil I getestet, jedoch unter veränderten Beleuchtungsverhältnissen. In dem 48tägigen Versuchsteil II war die Beleuchtungsstärke der belohnten Seite auf 350 Lux erhöht. 3 der bereits im Versuchsteil I untersuchten Tiere erreichten diesmal das Lernkriterium, und zwar nach 19 (T 2) bzw. 28 (T 1 und T 4) Tagen (Abb. 4b). Ein VT dieser Gruppe (T 3) starb vor Erreichen des Lernkriteriums. Wie die sequenzanalytische Auswertung aber zeigt (Abb. 5), wird von diesem Maulwurf nach dem 93. Lauf im

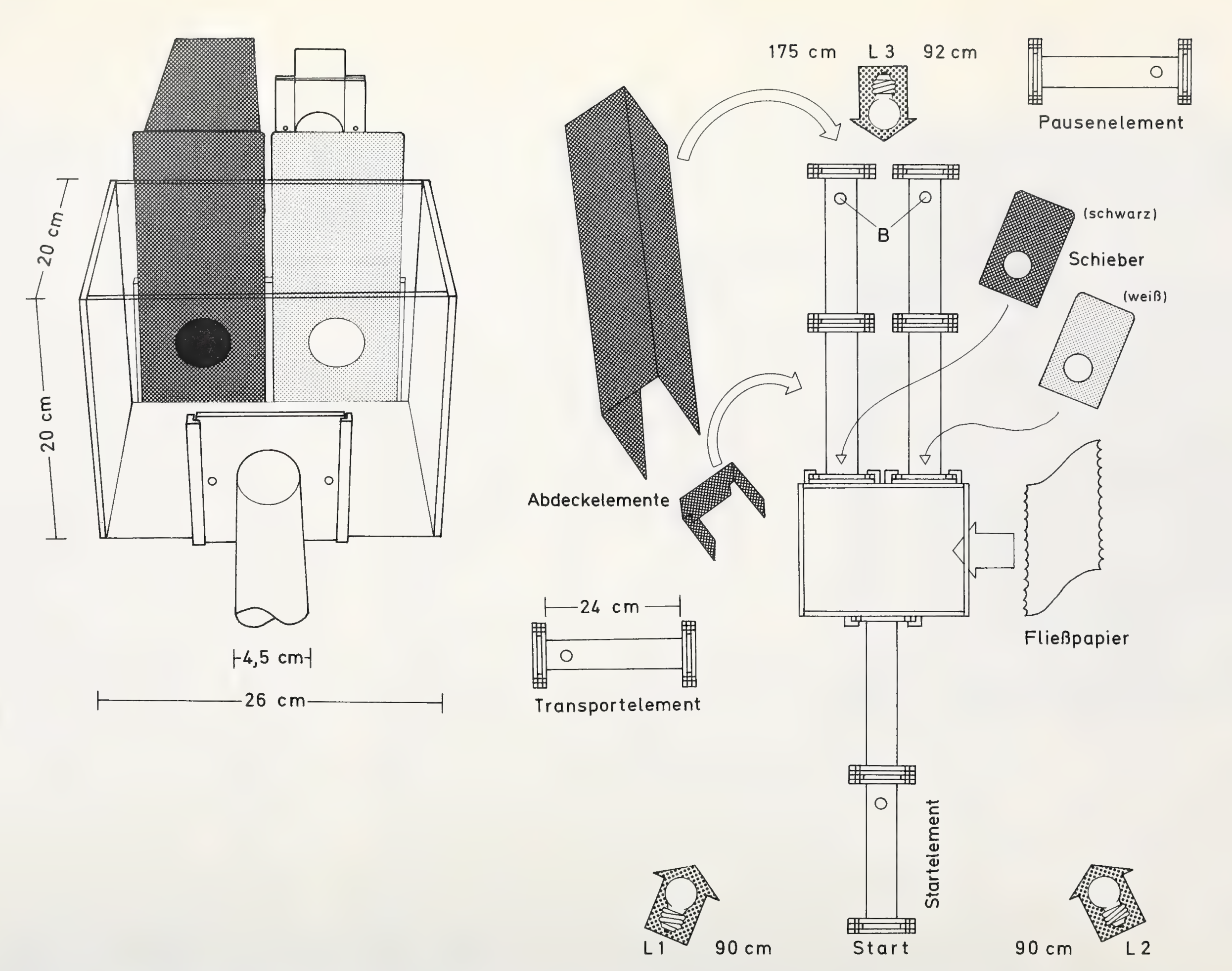


Abb. 3. Schemazeichnung der Zweifachwahlapparatur. *Links:* schräge Aufsicht auf den Entscheidungskasten (a); *rechts:* Aufsicht auf die vollständige Versuchsanlage (b). L 1, L 2, L 3: 100-Watt-Glühlampen und deren Lichteinfallsrichtung (Rasterpfeile). L 1 und L 2 sind mit konstantem Abstand (90 cm) vom Mittelpunkt der Wahlseite angebracht und leuchten diese von vorn gleichmäßig aus. L 3 beleuchtet die Apparatur von hinten und ist der einzustellenden Beleuchtungsstärke gemäß 175 cm bzw. 92 cm von den rückwärtigen Röhrenenden entfernt. B = Belohnungsloch, es wird nur zum Anbieten einer Mehlkäferlarve als Futterbelohnung geöffnet

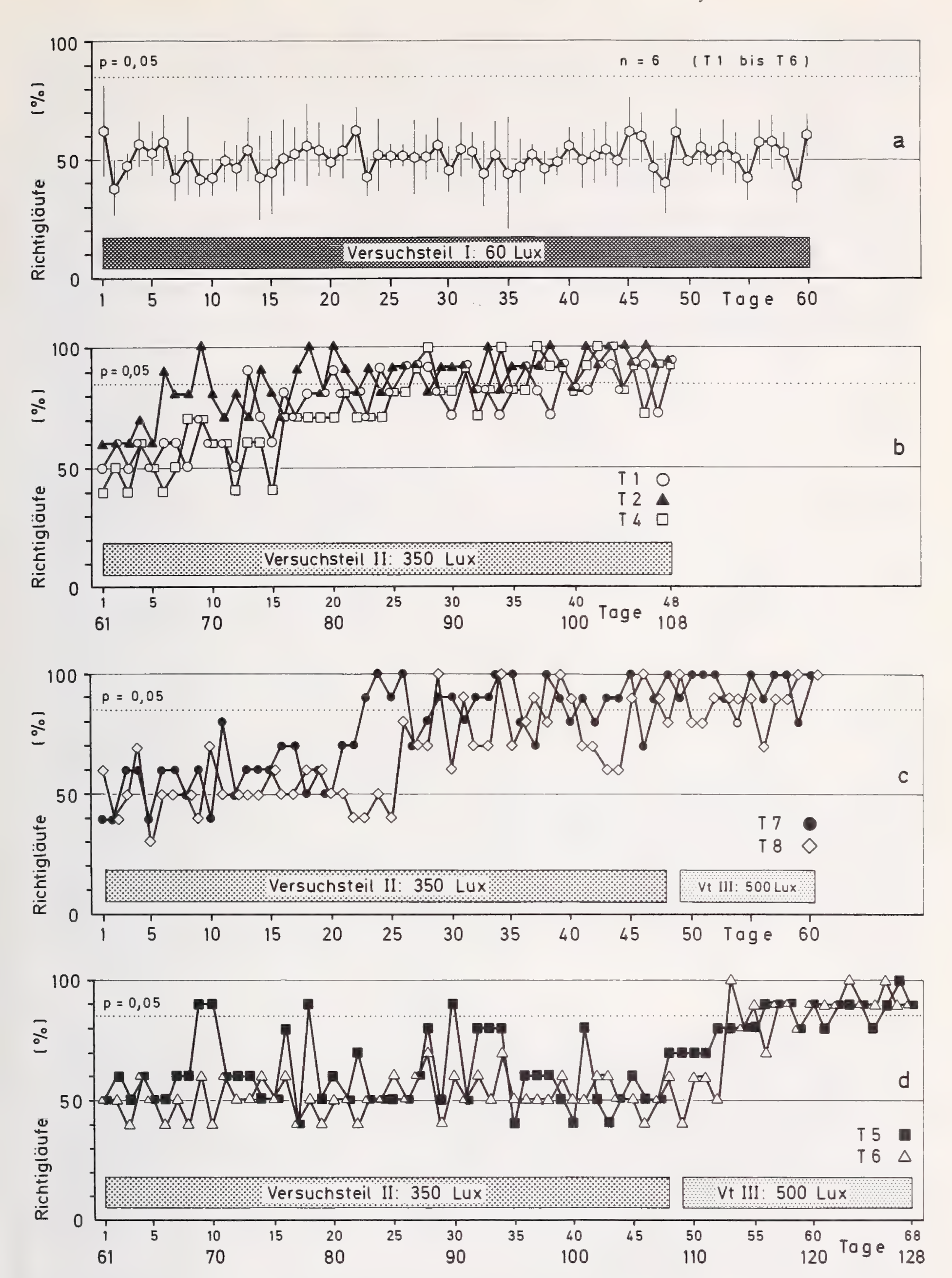


Abb. 4. Kurven der Richtigläufe (RL) für die Dressur auf Hell-Dunkel-Unterschiede bei verschiedenen Beleuchtungsstärken: Versuchsteil I (60 Lux), Versuchsteil II (350 Lux) und Versuchsteil III (500 Lux). (a) Mittelwertskurve der RL von 6 Maulwürfen (T 1 bis T 6) während des Versuchsteils I; angegeben ist die Standardabweichung. (b) Einzellernkurven von 3 Maulwürfen (T 1, T 2, T 4), die bereits Versuchsteil I absolviert haben. (c) Einzellernkurven von 2 bisher versuchsunerfahrenen Maulwürfen (T 7, T 8). (d) Einzellernkurven der Maulwürfe T 5 und T 6, deren Dressur wie bei T 1, T 2 und T 4 mit Versuchsteil I begonnen hat. Gepünktelte Linie: Signifikanzgrenze (p = 0,05: Prüfung einer Grundwahrscheinlichkeit nach KOLLER 1969)

Versuchsteil II die Annahmegrenze (90 % RL, p = 0,05) für das Eintreten des Lernerfolges erreicht. Das bedeutet, auch für den Maulwurf T 3 ist das Ergebnis der Dressur auf Hell-Dunkel-Unterschiede positiv zu werten. 2 bisher versuchsunerfahrene Tiere (T 7 und T 8) benötigten bis zum Erreichen des Lernkriteriums 25 (T 7) bzw. 39 (T 8) Tage (Abb. 4c).

Versuchsteil III: Die Beleuchtungsstärke auf der belohnten Seite betrug im Anschluß an den Versuchsteil II vom 49. (Abb. 4c) bzw. 109. Tag (Abb. 4d) an 500 Lux. 2 Maulwürfe (T 5 und T 6), die als einzige die Aufgabe bisher nicht gelernt hatten, erfüllten unter diesen Beleuchtungsverhältnissen rasch das Lernkriterium, der eine (T 6) nach 7, der andere (T 5) nach 10 Tagen (Abb. 4d). Die Lernkurven derjenigen VT, welche im Versuchsteil II das Lernkriterium bereits erreicht hatten, näherten sich jetzt in der Anzahl der RL dem 100 %-Niveau an (T 7 und T 8 in Abb. 4c).

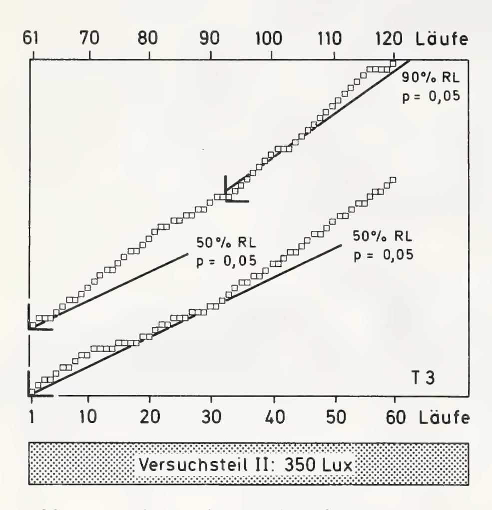


Abb. 5. Lernkurve des Maulwurfs T 3 (sequenzanalytische Darstellung der Richtig- und Falschläufe nach HARDER et al. 1972), der nach dem 12. Tag (120. Lauf bzw. Durchgang) im Versuchsteil II gestorben ist. *Unten:* Lauf 1 bis 60; *oben:* Lauf 61 bis 120

Diskussion

Trotz zahlreicher Untersuchungen, die zu einer weitgehenden Strukturaufklärung des Maulwurfsauges geführt haben, ist auf experimenteller Grundlage bislang kaum etwas darüber bekannt, ob *Talpa europaea* zu Sehleistungen fähig ist und gegebenenfalls den optischen Sinn situationsspezifisch einsetzt.

In der vorliegenden Arbeit war es möglich, mit Hilfe einer speziellen Zweifachwahlapparatur nach der Vorgehensweise einer operanten Konditionierung Maulwürfe auf Hell-Dunkel-Unterschiede zu dressieren. Wie die Lernkurven zeigen, kann *Talpa europaea* Helligkeitsdifferenzen wahrnehmen und diese – wenn sie nicht zu gering sind – in der spezifischen Lernsituation als Orientierungsmerkmale nutzen. Im Gegensatz zu LUND und LUND (1965) ist hier in den Lernkurven eine stabile Kannphase ausgebildet (Abb. 4b bis c). Die zur optischen Orientierung erforderliche Unterschiedsschwelle ist individuell verschieden; 6 Maulwürfe erlernten die Aufgabe bei einer Beleuchtungsstärke von 350 Lux auf der hellen Seite, 2 Tieren war dies erst nach Erhöhung der Beleuchtungsstärke auf 500 Lux möglich (Abb. 4d). Eine Beleuchtungsstärke von 60 Lux erwies sich als unterschwellig und konnte von keinem der getesteten Maulwürfe als Orientierungszeichen eingesetzt werden (Abb. 4a). Hinweise auf eine Orientierung nach Infrarotstrahlen, wie sie für die Vampirfledermaus *Desmodus rotundus* nachgewiesen ist und in ihrer Bedeutung diskutiert wurde (SCHMIDT und MANSKE 1982; KÜRTEN und SCHMIDT 1982), ergaben sich für *Talpa europaea* in diesen Versuchsreihen nicht.

Offen bleibt die Frage nach der Funktion des optischen Sinnes von *Talpa europaea*. Es ist bekannt, daß der europäische Maulwurf einen Teil seiner Aktivitätsphasen oberirdisch verbringt (MORRIS 1966). Zahlreiche zufällige Einzelbeoachtungen verdeutlichen in ihrer Gesamtheit, daß diese Tiere regelmäßig zu jeder Jahres- und Tageszeit ihren unterirdischen Bau verlassen und auf der Erdoberfläche tätig werden (u. a. REMUS 1901; HAUCHECORNE 1927; SCHAERFFENBERG 1940; HORNUNG 1942; NIETHAMMER 1963). Sie weichen vor Überschwemmungen ihrer Tunnelsysteme (teils schwimmend) auf höher gelegene Gelän-

deabschnitte aus und kehren nach Rückgang der Fluten rasch wieder zu ihren ehemaligen Wohngebieten zurück (Csizmazia 1982; Johannesson-Gross und Gross 1986). Auch ihr Nachweis im Beutespektrum von Greifen und Eulen bestätigt indirekt ebenfalls Oberflächenaktivitäten (z.B. Southern 1954; Skoczen 1962).

Welche Sinne den Maulwurf außerhalb seines Baues leiten, ist weitgehend unbekannt. Gehör, Geruch, Erschütterungs- und Tastsinn werden als vorrangig betrachtet (Herter 1957). Eine optische Orientierung scheint – wenn überhaupt – von untergeordneter Bedeutung zu sein. Dies schon deswegen, da aus anatomischen Gründen ein Verlust des Bildsehens angenommen werden muß. Diejenigen Teile des Auges, die zum Hervorbringen eines scharfen Bildes auf der Retina notwendig sind (Cornea, Linse, Glaskörper), werden von ihrer Ausbildung her dieser Aufgabe nicht mehr gerecht (Sokolowa 1964; Quilliam 1966c). Siemen (1976) weist in diesem Zusammenhang zusätzlich auf Degenerationserscheinungen der Netzhaut hin.

Der optische Sinn vieler Säugetiere ist aber nicht nur für ein Zurechtfinden im Raum wichtig, ebenso bedeutungsvoll ist er für die Orientierung in der Zeit (Hoffmann 1981).

Maulwürfe lassen einen 24-Std.-Rhythmus ihrer lokomotorischen Aktivität erkennen, der zusätzlich von Kurzzeitzyklen überlagert sein kann (z.B. Godfrey 1955; Mellanby 1967; Meese und Cheeseman 1969). Ergebnisse einer über 12 Monate durchgeführten Studie zur Tagesaktivität von *Talpa europaea* durch Woods und Mead-briggs (1978) legen die Vermutung nahe, daß die auftretenden Aktivitätsschübe vom täglichen Lichtgang und seiner Änderung im Jahresverlauf beeinflußt werden. Aber nicht nur hinsichtlich tagesrhythmischer Vorgänge scheint das Licht bei diesen Tieren eine Rolle zu spielen, sondern möglicherweise auch bei der zeitlichen Einnischung des Fortpflanzungsverhaltens in das Jahresgeschehen. *Talpa europaea* ist eine monöstrische Art mit einer nur relativ kurzen Brunftzeit im Frühjahr (Matthews 1935; Deanesly 1966). Auch wenn man unterstellt, daß dem Fortpflanzungszyklus des Maulwurfs ein circannualer Rhythmus zugrunde liegt, erscheint die Photoperiode in den gemäßigten Breiten mit ihrer störungsfreien Information als Zeitgeber zur Synchronisation der Brunftzeit geeignet und notwendig. Der optische Sinn von *Talpa europaea* mag also weniger der räumlichen als vielmehr der zeitlichen Orientierung dienen. Die hierzu erforderliche Kontrolle des Lichtganges im Tages- und Jahresverlauf ist den Tieren möglich; sie sind, wie in den Lernversuchen gezeigt werden konnte, zur Lichtperzeption fähig, und sie können diese Fähigkeit auch nutzen, da sie sowohl in ihren Gängen oberflächennah vorkommen als diese auch regelmäßig verlassen, um oberirdisch aktiv zu werden.

Zusammenfassung

Untersucht wurde die Fähigkeit zur Hell-Dunkel-Diskrimination von *Talpa europaea* L. Mit einer speziellen Lernapparatur in Form eines modifizierten Röhrenlabyrinthes war es möglich, durch Futterbelohnung positiv verstärkte Zweifachwahlen auf Hell (belohnt) gegen Dunkel (unbelohnt) durchzuführen. Wie die Lernkurven zeigen, ist *Talpa europaea* fähig, Helligkeitsunterschiede wahrzunehmen. Sind sie nicht zu gering, werden sie in der Lernsituation als Orientierungsmerkmal eingesetzt. Von 8 VT (Wildfänge verschiedenen Alters und beiderlei Geschlechts, die zu Versuchsbeginn handzahm waren) erlernten 6 Maulwürfe die Aufgabe bei einer Beleuchtungsstärke von 350 Lux auf der hellen (belohnten) Seite, während 2 weitere Tiere das Lernkriterium (90 % RL an 3 aufeinanderfolgenden Tagen) erst nach Erhöhung der Beleuchtungsstärke auf der belohnten Seite von 350 Lux auf 500 Lux erreichten. Welche Bedeutung der Lichtwahrnehmung bei der weitgehend unterirdischen Lebensweise von *Talpa europaea* zukommt, wird diskutiert.

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Anschrift der Verfasserin: Dr. KRISTINA JOHANNESSON-GROSS, Kimpelstraße 8, D-3500 Kassel, FRG

Z. Säugetierkunde 53 (1988) 202–209
© 1988 Verlag Paul Parey, Hamburg und Berlin
ISSN 0044-3468

Vorkommen und Zug der Rauhhautfledermaus (*Pipistrellus nathusii* Keyserling und Blasius, 1839) in Baden-Württemberg

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Eingang des Ms. 15. 5. 1987

Abstract

The occurrence and migration of Nathusius' pipistrelle (Pipistrellus nathusii Keyserling & Blasius, 1839) in Baden-Württemberg

During the whole year Nathusius' pipistrelle can be found in southwest Germany, but not one record of reproduction is known from Baden-Württemberg. *Pipistrellus nathusii* is much more frequent in autumn and late summer (about 85 % of all records) than in other seasons. Therefore it is supposed, that this species is normally migratory in southwest Germany and hibernates there only seldom, but more in southern countries (e.g. France). It could be shown that Nathusius' pipistrelle arrives 10 days earlier at the north eastern part of Baden-Württemberg than at Lake Konstanz and about four weeks earlier than at the Regio Basiliensis. A possible migration route is discussed.

Einleitung

Die Analyse saisonaler Wanderungen von Fledermäusen ist durch die nächtliche und oft versteckte Lebensweise und durch die Seltenheit der Tiere erschwert.

Rauhhautfledermäuse überwintern in der Regel nicht in Felshöhlen und sind dadurch gezwungen, weiträumige Wanderungen durchzuführen (Roer 1971), die sie in Gebiete leiten, deren durchschnittliche Tagestemperaturen im Januar −6 °C nicht unterschreiten (Strelkov 1969). Der Verbreitungsschwerpunkt der Art liegt im zentralen und südlichen Rußland (Strelkov 1969; Roer 1974; Hanak und Gaisler 1976; Claude 1976), von wo Wanderungen zum Kaukasus und auf den Balkan bis nach Griechenland belegt sind (Strelkov 1969). Untersuchungen über das Vorkommen in den westlichen Randgebieten liegen aus der DDR (Heise 1982), der Tschechoslowakei (Hanak und Gaisler 1976) und aus Österreich (Bauer und Wirth 1979) vor. Für andere mitteleuropäische Länder stellten Roer (1974, 1976) und Kock und Schwarting (1987) zahlreiche Nachweise zusammen.

In der vorliegenden Arbeit wird versucht, das Vorkommen der Rauhhautfledermaus in Südwest-Deutschland zu beschreiben und aus der Verteilung der Funddaten Hinweise auf Wanderungen dieser Art zu erhalten. Unterschiedliche Zugzeiten von Männchen und Weibchen, wie sie von Strelkov (1969) und Heise (1982) vermutet werden, wurden nicht berücksichtigt.

Material und Methoden

Für die Auswertung wurden die Publikationen von Claude (1976), Stutz und Haffner (1985) sowie die Daten der Fledermauskartierung in Baden-Württemberg (Kulzer et al. 1987) herangezogen. Zum Vergleich dazu wurden Mitteilungen aus anderen Gebieten Deutschlands berücksichtigt (Tab. 1). Es standen Daten von 135 Fundorten mit insgesamt 508 Tieren zur Verfügung. 326 Tiere wurden allein aus Baden-Württemberg und dem Deutsch-Schweizer Grenzgebiet gemeldet.

Zur Darstellung der Wanderung wurde Baden-Württemberg in vier Sektoren eingeteilt, deren Grenzen sich an geographischen Merkmalen (Schwarzwald, Schwäbische Alb) und an Orten mit Fundhäufungen orientierten (Abb. 1). Es wurden nur Funde gewertet, von denen mindestens der

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Tabelle 1. **Anzahl der Funde von Rauhhautfledermäusen in verschiedenen Gebieten Deutschlands**

Gebiet	Anzahl Fundorte	Anzahl Tiere	Quelle
Baden-Württemberg und Deutsch-Schweizer Grenzgebiet	91	326	CLAUDE 1976; GEBHARD 1983; MÜLLER und WIDMER 1983; STUTZ und HAFFNER 1985; KULZER et al. 1987
Rhein-Main-Gebiet	34	157	KOCK 1981; KOCK und SCHWARTING 1987
Nordrhein-Westfalen	5	20	ROER 1976; VIERHAUS und BÜLOW 1978
Schleswig-Holstein	5	5	DIETERICH 1982
Summe	135	508	

Monat bekannt war. Der Erfassungszeitraum erstreckte sich für Baden-Württemberg von 1962 bis 1986. Die übrigen Funde gehen bis in das Jahr 1908 zurück. Für die Berechnung der Zugdaten wurde der Juli als erster Monat gewertet (der Monat mit den wenigsten Funden). Für jeden Sektor wurde die Gesamtsumme der in einem Monat gemeldeten *Pipistrellus nathusii* (ohne Berücksichtigung der Jahreszahl) sowie der Median und das 95 %-Konfidenzintervall aller Funde ermittelt. Für die Berechnung der Medianwerte wurden nur die Funde berücksichtigt, von denen das exakte Datum bekannt war. Die Fundverteilung im Sektor III war zweigipfelig, in allen anderen Fällen eingipfelig, so daß zur Berechnung des Medians im ersten Fall nur die Funde in den Monaten Juli bis Dezember, sonst die des ganzen Jahres berücksichtigt wurden. Die in der vorliegenden Untersuchung berechneten Mediane sind somit stets als Indices für Durchzugszeiten im Herbst zu werten.

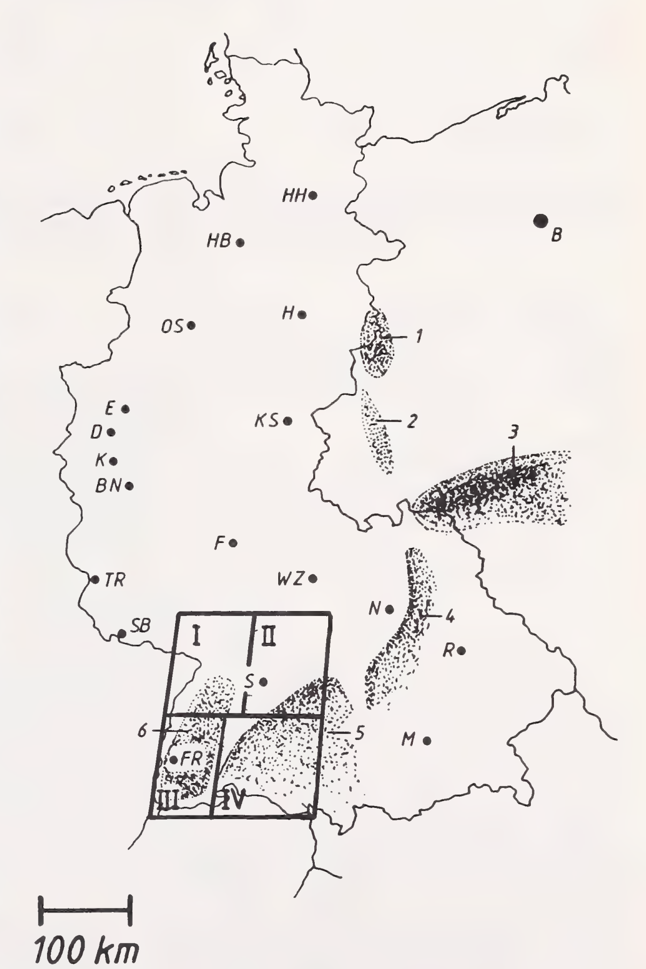


Abb. 1. Aufteilung der Fläche Baden-Württembergs in vier Sektoren (I–IV). Lage der zur Interpretation des Herbstzuges wichtigen Gebirge: 1 = Harz; 2 = Thüringer Wald; 3 = Erzgebirge; 4 = Fränkische Alb; 5 = Schwäbische Alb; 6 = Schwarzwald

Ergebnisse

Jahreszeitliche Verteilung der Funde in Baden-Württemberg

In Baden-Württemberg und dem Deutsch-Schweizer Grenzgebiet wurde *Pipistrellus nathusii* in allen Mo-

naten nachgewiesen. 84,6 % (= 215 Tiere) aller Nachweise entfielen jedoch auf die Monate September bis Februar. Nur 10 Tiere (= 3,9 %) wurden in der Zeit von Juni bis August gefunden (Tab. 2). Die Verteilung der Funddaten ist ungleichmäßig (χ^2 = 209,8; p < 0,001). Der Median des vom 1.7 bis 30.6 gewerteten Jahres errechnet sich für Baden-Württemberg auf den 5. November (95 %-Konfidenzintervall: 25. 10.–21. 11.; Tab. 3). Das zweite schwach ausgebildete Fundmaximum im Spätwinter (Januar/Februar; Abb. 2) beeinflußt den Medianwert nicht. Die Befunde deuten auf eine saisonale Wanderung der Rauhhautfledermaus in Baden-Württemberg hin.

Tabelle 2. **Verteilung der in Baden-Württemberg gefundenen Rauhhautfledermäuse auf die vier Sektoren der Abb. 2**

Bereich	Monat												
	1	2	3	4	5	6	7	8	9	10	11	12	Summe
I	5	5	1									5	16
II	4	1			1				15	20			41
III	5	9	10	1	1	1			5	6	13	3	54
IV	13	8	2	8	5	2	2	5	43	26	15	14	143
Summe	27	23	13	9	7	3	2	5	63	52	28	22	254

I = Nordbaden; II = Unterfranken und Neckar-Raum um Tübingen und Stuttgart; III = Südbaden und Raum Basel; IV = Bodenseeraum und Schweizer Grenzgebiet. Unberücksichtigt ist die große Männchengruppe aus Büsingen (Kreis Waldshut; Müller und Widmer 1983).

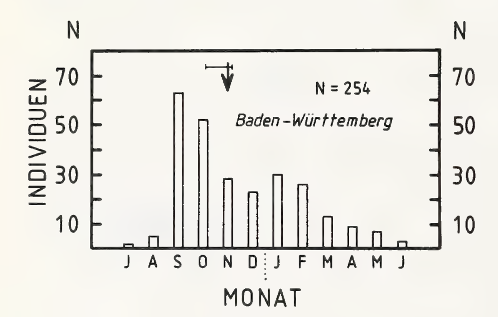


Abb. 2. Jahreszeitliche Verteilung der Rauhhautfledermausfunde in Baden-Württemberg. Aufgetragen ist die Zeit von Juli bis Juni. Nicht berücksichtigt wurde eine große Männchengesellschaft in einem Zwischenquartier in Büsingen (Müller und Widmer 1983). ↓: Median; ├─┤: 95 %-Konfidenzintervall

Regionale Zugmuster

Sowohl im Neckartal von Stuttgart und Tübingen, als auch im Bodenseeraum wurden in den Monaten September und Oktober die meisten Tiere gemeldet (Abb. 3). Das Neckartal erreichen die Rauhhautfledermäuse jedoch im Mittel 10 Tage früher als den Bodensee (p < 0,05; Median-Test; Tab. 3). Dort können die Tiere auch ganzjährig beobachtet werden, während im Neckartal außerhalb der Herbstmonate nur noch im Januar und Februar Tiere gemeldet wurden. Am Bodensee veranlaßt möglicherweise das warme Klima die Tiere zur Rast. Funde von bis zu 14 Tieren in den Monaten Dezember, Januar und Februar (Tab. 2) lassen zudem vermuten, daß Rauhhautfledermäuse dort auch überwintern.

In der Region Basel ist die Anzahl der Funde in den Monaten November und März maximal. Der Zugmedian fällt auf den 7. 11. (95 %-Konfidenzintervall: 21. 10.–16. 11.; Tab. 3) und damit drei Wochen später als im Bodenseegebiet (p < 0,05; Median-Test; Tab. 3). Aus Nordbaden sind bisher noch keine Herbstnachweise bekannt. Die geringe Anzahl der Funde läßt keine Aussagen über jahreszeitliche Zugbewegungen der Art in diesem Landesteil zu.

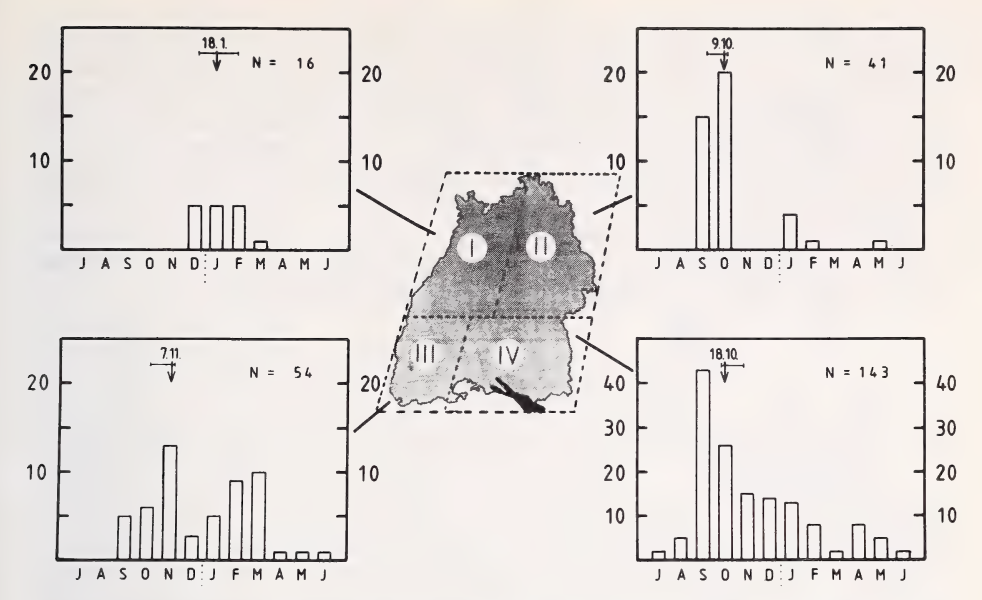


Abb. 3. Die Anzahl der je Monat mitgeteilten Rauhhautfledermäuse in den vier Sektoren Baden-Württembergs. In jedem Diagramm ist die Anzahl der berücksichtigten Funde (N), der Median des Herbstmaximums (↓) und das 95 %-Konfidenzintervall (⊢⊣) eingezeichnet

Das Vorkommen in anderen Gebieten Deutschlands

Umfangreiches Datenmaterial ist aus dem Rhein-Main-Gebiet bekannt (Kock 1981; Kock und Schwarting 1987), wo seit 1908 insgesamt 157 *Pipistrellus nathusii* beobachtet wurden. In der Regel fand man sie in Nistkästen. Auch dort wurden im September die meisten Tiere festgestellt (70 % aller Funde, Abb. 4). Die restlichen Mitteilungen konzentrierten sich nahezu zur Hälfte auf die Monate Januar und Februar. Nur 25 Tiere (= 15,9 %) fand man in der übrigen Zeit. Auch ein weiterer Befund spricht für eine nur kurzzeitige Belegung der Quartiere. In den Kästen, in denen im September Rauhhautfledermäuse vorgefunden wurden, befand sich 2–3 Wochen vorher nicht einmal Fledermauskot (Schwarting, mündl. Mitt.).

Tabelle 3. **Medianwerte und 95 %-Konfidenzintervalle der in den vier Bereichen Baden-Württembergs gefundenen Rauhhautfledermäusen, bezogen auf das am 1. Juli beginnende Jahr**

Bereich	Median $\tilde{x}$	95 %-Konfidenz-intervall
I	18. 1.	28. 12.–11. 2.
II	9. 10.	29. 9.–19. 10.
III	7. 11.	21. 10.–16. 11.
IV	18. 10.	12. 10.–16. 11.
Gesamt	5. 11.	25. 10.–21. 11.

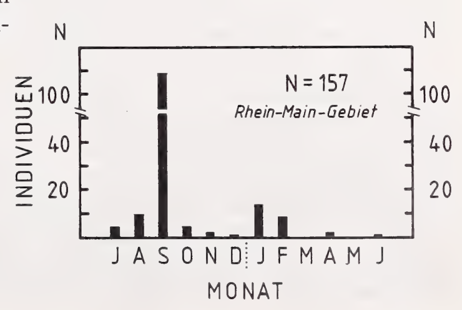


Abb. 4. Jahreszeitliche Verteilung von im Rhein-Main-Gebiet gefundenen Rauhhautfledermäusen (nach: Kock und Schwarting 1987). Aufgetragen ist die Zeit von Juli bis Juni

Nur wenige Daten liegen aus anderen Bundesländern vor. VIERHAUS und BÜLOW (1978) berichten außer von 3 älteren Funden (je ein Tier im August, September und November) von 16 Rauhhautfledermäusen in Nordrhein-Westfalen. Diese wurden an zwei Septembertagen in Nistkästen angetroffen. Wenige Tage später waren alle Kästen leer. ROER (1976) beobachtete im November eine Rauhhautfledermaus an den Krickenbecker Seen (Kreis Viersen). Aus Schleswig-Holstein sind bisher 5 Funde in den Monaten September und Oktober bekannt (DIETERICH 1982).

Alle Funde aus diesen Bundesländern stimmen mit den Fundhäufungen in Baden-Württemberg und dem Deutsch-Schweizer Grenzgebiet gut überein. Sie deuten ebenfalls auf einen Herbstzug der Rauhhautfledermaus in der Bundesrepublik hin.

Diskussion

Rauhhautfledermäuse sind zu weiträumigen Wanderungen fähig (STRELKOV 1969; ROER 1974, 1976; CLAUDE 1976; DIETERICH 1982; KOCK und SCHWARTING 1987), was bisher durch etwa 25 Fernfunde (>100 km) belegt ist. In Deutschland kann die Art in allen Monaten beobachtet werden, wenngleich sie im Herbst und Winter sehr viel häufiger ist (Abb. 2 und 4). Überwinternde Tiere sind wiederholt festgestellt worden (z. B. KULZER et al. 1987), Wochenstuben sind dagegen bis auf eine Ausnahme (ISSEL et al. 1977) aus diesem Jahrhundert nicht bekannt. Auch andere Sommernachweise sind spärlich. Dagegen ist die Art in Berlin und der DDR stellenweise sogar häufig (SCHMIDT 1977, 1978; HEISE 1982; HIEBSCH 1983). Die von KLAWITTER (1974) festgestellte hohe Dichte von *Pipistrellus nathusii* in West-Berlin könnte jedoch gleichfalls ziehende Tiere betreffen, da Rauhhautfledermäuse auch hier besonders häufig im September gefunden wurden.

In der DDR beringte Rauhhautfledermäuse zeigen eine deutliche SW bis SSW orientierte Wegzugrichtung, wie durch Ringfunde aus der Bundesrepublik Deutschland, der Schweiz und Frankreich belegt ist (Zusammenfassung bei KOCK und SCHWARTING 1987).

Die Rauhhautfledermäuse verlassen ihre Fortpflanzungsquartiere in den Monaten August bis Oktober; im Winter fehlen sie in der DDR weitgehend (SCHOBER 1960; HAENSEL 1967; SCHMIDT 1978; HEISE 1982). Nimmt man einen Wegzug im September an, wobei die ♀ möglicherweise vor den ♂ abziehen (STRELKOV 1969; HEISE 1982), könnten diese Fledermäuse in den Monaten September/Oktober im Neckartal und am Bodensee eintreffen. Das weitgehende Fehlen in anderen Teilen der Bundesrepublik ließe sich mit einer angestammten Zugrichtung SW bis SSW und der Leitwirkung der Mittelgebirgszüge erklären. Die Funde in den Niederlanden (WIJNGAARDEN et al. 1971) deuten jedoch auch auf einen, möglicherweise schwächeren Zug durch die norddeutsche Tiefebene hin.

Bei der nach SW gerichteten Wanderung würden die meisten aus der DDR und Polen kommenden Rauhhautfledermäuse nach Umgehung des Harzes, des Thüringer Waldes und des Erzgebirges zwangsläufig in den Main-Neckar-Raum fliegen. Im SW schließt sich dann ein nach NNO geöffneter Gebirgstrichter an (im W der Schwarzwald, im O die Schwäbische und Fränkische Alb). Auf diesem hypothetischen Zugweg (Abb. 5) könnten die Rauhhautfledermäuse schließlich das klimatisch günstige Bodensee-Hochrhein-Gebiet erreichen. Im weiteren Zugverlauf müßten sich die Tiere dann SW oder W orientieren und dabei entweder durch das Schweizer Mittelland, entlang des Genfer Sees, des Rhône-Tals nach Südfrankreich oder im weiteren Verlauf des Hochrheines durch die Burgundische Pforte in das Rhône-Tal fliegen. Das im November beobachtete Zugmaximum in der Baseler Gegend macht den zweiten Zugweg wahrscheinlich. Widersprüchlich dazu sind allerdings die Angaben von AELLEN (1961), der die Tiere am Bergpaß Col de Bretolet hauptsächlich im September gefangen hat. Möglicherweise werden dort Tiere gefangen, die aus südlicheren Wochenstubenpopulationen stammen.

Zu berücksichtigen ist bei allen Überlegungen, daß die Art entlang des gesamten Weges

überwintern kann, sowohl in den Höhlen der Schwäbischen Alb (KULZER et al. 1987), als auch in Baumhöhlen oder Nistkästen (FELTEN und KLEMMER 1960; ROER 1976; KOCK 1981; KOCK und SCHWARTING 1987).

Der Rückzug in die Sommerquartiere ist in der Funddatenverteilung nicht klar zu erkennen, da der Nebengipfel (Abb. 2) zwei Interpretationen zuläßt: Es kann sich einerseits um Meldungen von Tieren handeln, die auf dem Heimzug in die Sommerquartiere sind. Es könnte sich aber auch um eine durch äußere Bedingungen (z.B. Kälteeinbruch) verursachte Häufung von Funden am Ort überwinternder Tiere handeln.

In Sommerquartieren bei Halle wurden die ersten Tiere Anfang April festgestellt (SCHOBER 1960); andere Autoren geben als frühestes Ankunftsdatum in der DDR Anfang Mai an (SCHMIDT 1978; HEISE 1982). Damit wird ein „Frühjahrszug“ in Baden-Württemberg im Januar unwahrscheinlich.

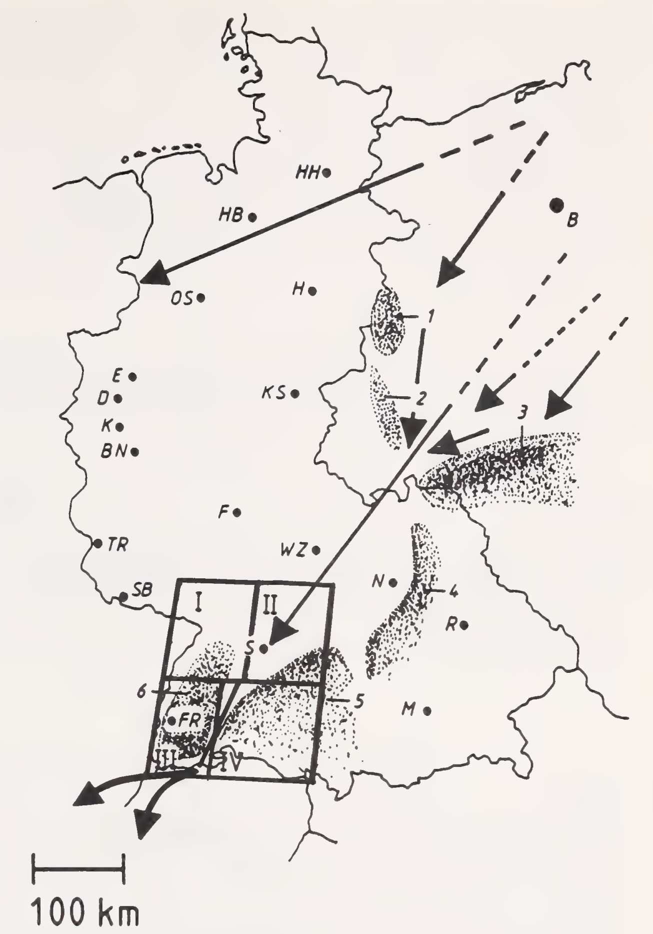


Abb. 5. Hypothetischer Zugweg der Rauhhautfledermaus aus potentiellen Wochenstubenquartieren in der DDR und Polen. Angenommen wird eine angeborene Herbstzugrichtung nach SW bis SSW, was von Ringfunddaten in dieser Richtung belegt wird. Abkürzungen wie in Abb. 1

Die relativ häufigen Funde könnten dagegen durch verschärfte Kälteperioden verursacht worden sein. Sie können bei überwinternden Tieren zur Unterbrechung des Winterschlafes und zur Suche nach geschützteren Quartieren führen. Gerade in Baumhöhlen überwinternde Fledermäuse sind dadurch sehr gefährdet (KULZER 1986). Die Tatsache, daß viele der im Januar und Februar gefundenen Rauhhautfledermäuse geschwächt oder gar tot waren, unterstreicht diese Ansicht.

Die Frage, auf welchem Weg die Tiere in die Sommerquartiere zurückkehren, bleibt somit weiterhin offen. Das bei Basel festgestellte Fundmaximum im März kann durchaus mit einem Rückzug in Verbindung stehen, doch ist das Datenmaterial noch zu spärlich, um weitere Überlegungen anzustellen. GEBHARD (briefl. Mitt.) glaubt an einen geradlinigen, schnellstmöglichen Rückzug in die Sommerquartiere. In diesem Zusammenhang ist die Mitteilung einer aus 72 Tieren bestehenden Männchengesellschaft von *Pipistrellus nathusii* in der deutschen Exklave Büsingen (KreisWaldshut) von Bedeutung. Jahr für Jahr kamen die Tiere regelmäßig im April an und waren gegen Anfang Mai wieder verschwunden. Bei

einer durchschnittlichen Reisegeschwindigkeit von etwa 50 km/h (Kock und Schwarting 1987) würden die Tiere „termingerecht“ in den osteuropäischen Sommergebieten ankommen.

Die Rauhhautfledermäuse sind wahrscheinlich Saisonwanderer, die das Gebiet der Bundesrepublik überfliegen oder an wenigen besonders begünstigten Stellen überwintern. Die Art *Pipistrellus nathusii* fällt demnach auch unter die Bonner Konvention vom 23. Juni 1979 über das Übereinkommen zur Erhaltung wandernder wildlebender Tierarten (Erz 1981). In die rote Liste der gefährdeten Tiere und Pflanzen ist sie unter die Kategorie II (Gefährdete Durchzügler, Überwinterer, Übersommerer, Gäste usw.) einzuordnen (Blab et al. 1984).

Danksagung

Für die kritische Durchsicht des Manuskriptes danke ich den Herren Prof. Dr. E. Kulzer, Tübingen, Dr. H. Roer, Bonn, und J. Gebhard, Basel, sowie Frl. Anita v. Buch, Tübingen. Zudem bin ich noch einer Vielzahl von Fledermausforschern dankbar, die mir bereitwillig ihre Daten zur Verfügung gestellt haben.

Zusammenfassung

Anhand von Literaturdaten wird das Vorkommen der Rauhhautfledermaus in Baden-Württemberg beschrieben. Es wurden insgesamt 508 Funde ausgewertet. Dabei ergaben sich Fundhäufungen im Herbst und im Winter (Abb. 2). Während das Hauptmaximum im September mit einer Herbstwanderung in Verbindung gebracht werden kann, ist das Nebenmaximum im Januar eher auf Meldungen von Winterverlusten zurückzuführen. Es wird ein Zugweg von Sommerquartieren in der DDR oder Polen durch das Neckartal zum Bodensee und von dort aus weiter durch das Schweizer Mittelland oder die Burgundische Pforte in die Winterquartiere erwogen (Abb. 5). Offen bleibt die Frage, wann und auf welchem Weg die Tiere in die Sommerquartiere zurückkehren.

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Z. Säugetierkunde 53 (1988) 210–224

ISSN 0044-3468

The anatomy of the stomach and caecum of the Samango monkey, *Cercopithecus mitis erythrarchus* Peters, 1852

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Receipt of Ms. 12. 03. 1987

Abstract

An investigation of the gastric and caecal anatomy of *Cercopithecus mitis erythrarchus* revealed a simple glandular stomach and a sacculated caecum. The unilocular glandular stomach is typical of cercopithecine primates. The caecum and colon possess well-developed taeniae and haustra, and provide microhabitats for numerous symbiotic bacteria. The morphological observations are interpreted in terms of the functional digestive process of this primarily frugivorous primate.

Introduction

Herbivorous mammals can be classified into two broad categories according to their digestive strategy and gut adaptations that accommodate microbial fermentation (Parra 1978): firstly, those animals with an enlarged foregut that is the main site of microbial activity and in which microbial fermentation precedes gastric intestinal digestion, or secondly, those animals with an enlarged hindgut, in which gastric intestinal digestion of the diet occurs before microbial fermentation (Parra 1978). Many fermentative bacteria are cellulolytic, and for those animals with a diet rich in structural carbohydrates a large fermentation chamber in the digestive tract is necessary.

Old World monkeys of the subfamily Colobinae are predominantly folivorous (Chivers and Hladik 1980), and differ from all other primates in the large size and anatomical complexity of the stomach (Bauchop and Martucci 1968). Consequently, considerable literature has accumulated on the ruminant-like, microbial gastric digestion occurring in the stomach (Bauchop and Martucci 1968; Ohwaki et al. 1974; Bauchop 1978) and on the microbiology of the colobine stomach (Bauchop 1971).

The more typical Old World monkeys of the subfamily Cercopithecinae are predominantly frugivorous-omnivorous, and the stomach is a simple, smooth-walled sac (Hill 1958). Recent investigations on volatile fatty acid (VFA) concentrations (the breakdown products of microbial fermentation) and digesta movement in the gastrointestinal tracts of a number of Cercopithecinae (Clemens and Phillips 1980; Clemens and Maloiy 1981) have demonstrated that the stomach contains an acidic environment unsuitable for prolonged microbial activity. From the high concentrations of VFAs recorded in the large intestine of these primates, it appears that the caecum and colon are important sites of microbial activity and VFA production.

An extensive study on the socioecology and feeding ecology of the Samango monkey *Cercopithecus mitis erythrarchus* is currently in progress in Natal (Lawes pers. comm.). To examine the Samango in relation to the two digestive strategies and to relate the diet to current concepts of digestion theory, a detailed knowledge of the monkey's gastric morphology was required. A preliminary examination of the stomach and caecum of the Samango monkey was therefore initiated to determine the gross anatomy, histology and ultrastructure of the respective organs, and to correlate anatomy with diet and function.

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Materials and methods

One weaned juvenile female and one adult female Samango monkey were used for this examination. The shot animals were dissected in the field immediately after death and photographed to display the position of the organs in situ. The pH in the proximal and distal stomach regions, mid-region of the small intestine, caecum, and ascending and descending colon was measured using a single glass probe electrode (Model TC pH 800) placed in a small incision in the GIT wall.

Small sections of stomach and caecal tissue (5 mm × 5 mm) were fixed in 3 % buffered glutaraldehyde for scanning and transmission electron microscopy. Thereafter whole organs were placed in Bouin's fixative for 18 h. After fixation the organs were bisected and preserved in 70 % alcohol. One half of each organ was used for gross morphological analysis, the other for histological examination using standard tissue preparation techniques (Humason 1962). Haematoxylin and eosin were used as general tissue stains, while Alcian blue was used to confirm mucus (polysaccharide) secretion (Humason 1962).

For electron microscopy tissue was removed from the gut and postfixed in 1 % osmium tetroxide in 0,05 M sodium-cacodylate buffer, then dehydrated in a graded alcohol series. Material for transmission electron microscopy (TEM) was further dehydrated in propylene oxide and embedded in Epon. Sections were cut on an LKB Ultratome 3 ultramicrotome, stained with uranyl acetate and lead citrate and viewed with a Hitachi Model HU-11E-1 transmission electron microscope. For scanning electron microscopy (SEM), material was critical-point dried, coated with gold palladium and viewed with a Hitachi S-570 scanning electron microscope.

Results

pH

pH readings recorded at different sites along the GIT are given in the Table.

Table. **pH readings along the GIT of adult and juvenile Samango monkeys**

	Section of tract					
	Stomach		Mid small intestine	Caecum	Ascending colon	Descending colon
	Fundus	Antrum				
Adult	5.00	3.13	6.31	5.97	6.25	6.47
Juvenile	5.19	3.08	6.53	5.58	6.69	6.90

Topography in situ

The stomach of *C. m. erythrarchus* extends laterally across the abdominal cavity and occupies approximately one quarter by volume of the cavity. The small intestine, caecum, colon and rectum fill the remainder of the cavity (Fig. 1). The caecum is located in the lower right region of the abdominal cavity, lying directly against the abdominal wall (Fig. 1) and partially obscured in the distal region by the mesentery of the small intestine. The large, haustrated transverse colon is prominent, possessing distinct taeniae (Fig. 1) along its entire length.

Gross morphology

Stomach

The stomach is a simple unilocular glandular sac (Fig. 2a), with the oesophagus entering the mid-dorsal region of the corpus (forestomach). Sinistral to the gastro-oesophageal junction the fundus extends laterally, forming a slightly globular pouch. Dextral to the junction, the lesser curvature immediately reflects to form the pars pylorica (Fig. 2a); the antrum (hindstomach) extends from the oesophageal opening, and curves dorsally forming

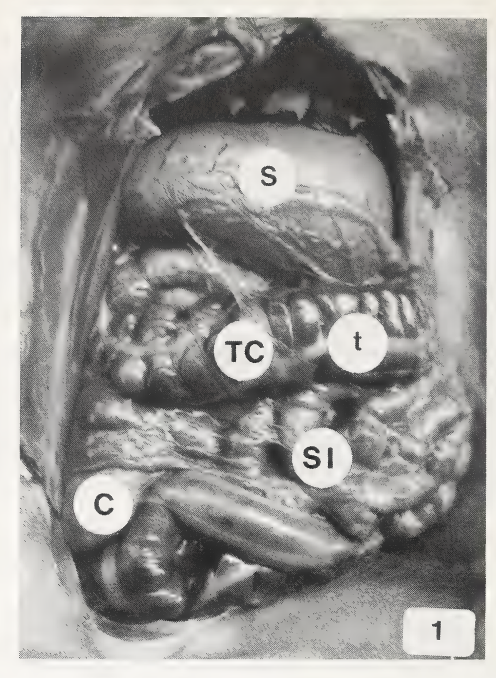


Fig. 1. The disposition of the GIT within the abdomen of *C. m. erythrarchus*. Note the haustrated transverse colon (TC) and the taenia (t). SI = small intestine, C = caecum, S = stomach

the pars pylorica. The only apparent difference between the stomachs of juvenile and adult monkeys was the increased folding of the stomach wall in the adult.

Caecum

The caecum of adult *C. m. erythrarchus* displays several haustrum-like sacculations and two prominent, laterally situated taeniae which extend along the length of the colon. The ileum enters the caecum at the border between the ampulla caeci and corpus caeci (Fig. 3). Distal to this opening at the end of the ampulla is the caecocolic junction, from which the proximal colon emerges (Fig. 3).

Although the general form of the adult and juvenile caeca is similar, they differ markedly in the extent of haustration and folding of the internal mucosal surface. In the adult (Fig. 3), a deep sacculation separates the corpus caeci and ampulla; it is likely that digesta is directed into the corpus caeci via a muscular valve at the ileocaecal junction (Fig. 3). The extent of the internal folding is similar in the caecum and proximal colon. The caecum of juveniles (Fig. 4), in comparison, is a large unilocular sac with no distinct separation between the corpus caeci and ampulla caeci.

Histology

Stomach

A typically mammalian gastric tissue plan (Weiss and Greep 1977; Ham and Cormack 1979) is present (Fig. 5). The muscularis externa is generally thicker in the corpus than in the antrum, where the circular muscle layer (stratum circulare) is approximately three times thicker than the longitudinal layer (stratum longitudinale).

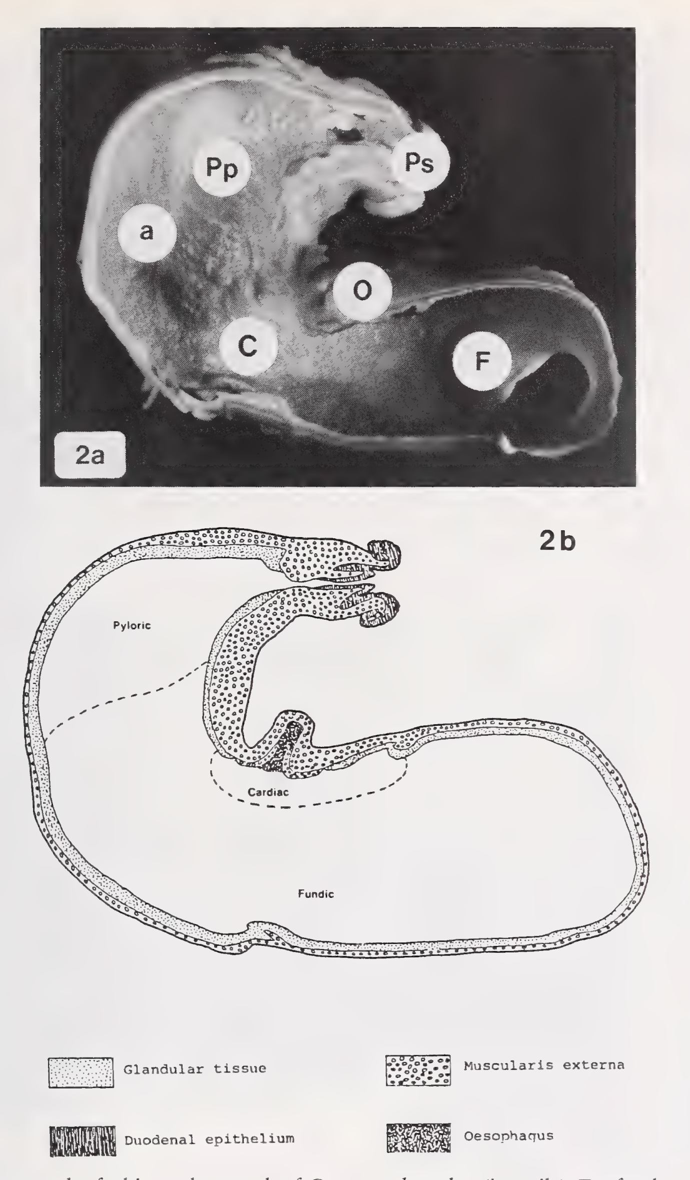


Fig. 2a. A photograph of a bisected stomach of *C. m. erythrarchus* (juvenile). F = fundus, C = corpus, Pp = pars pylorica, O = oesophagus, Ps = pyloric sphincter, a = antrum. – b: Semi-diagrammatic drawing of a bisected stomach showing the regions of glandular tissue

A submucosa of loose connective tissue is of constant thickness in the corpus and antrum (Fig. 5). The muscularis mucosa is continuous with that of the oesophagus, and lamina propria extends between the glandular tissue.

The mucosal lining of the stomach is histologically divisible into cardiac, fundic and pyloric regions. The cardiac tissue in the stomach extends 1–1,5 cm radially from the cardiac orifice (Fig. 2b). The short, branched cardiac glands possess wide foveolae with closely packed mucous neck cells (Fig. 6). These cells continue for some distance into the tubules of the glands. Parietal (oxyntic) and chief (or peptic or zymogen) cells are present

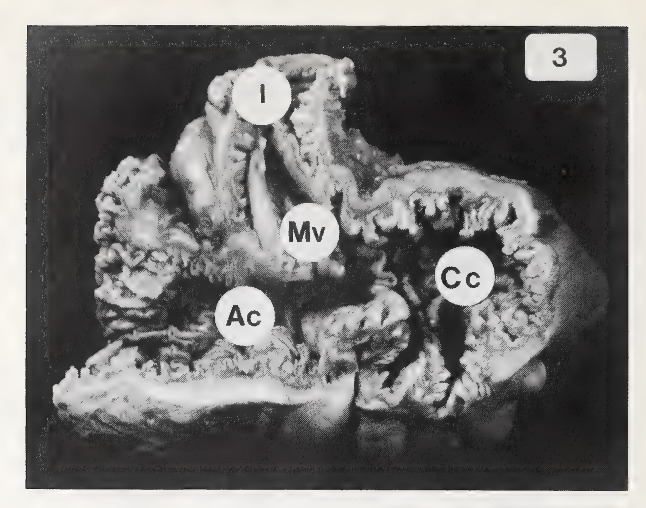


Fig. 3. A photograph of the bisected caecum of an adult *C. m. erythrarchus*, showing the deep haustration between corpus caeci (Cc) and ampulla caeci (Ac), and the muscular valve (Mv) at the ileocaecal junction. I = ileum

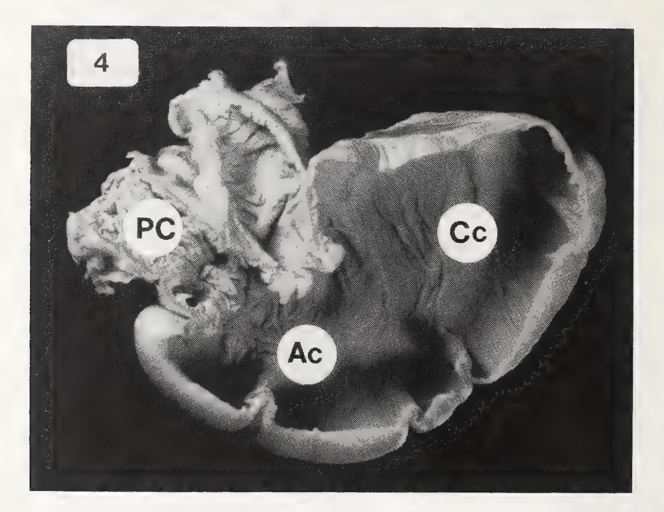


Fig. 4. A photograph of the bisected caecum of a juvenile *C. m. erythrarchus*. Cc = corpus caeci, Ac = ampulla caeci, PC = proximal colon

(Fig. 6), but their relative scarcity and the large numbers of closely packed mucous cells is characteristic of cardiac glands.

In the fundic region the glands are long and tubular with narrow foveolae and extend through the mucosa to the muscularis mucosa (Fig. 7). A histological stratification typical for mammalian fundic glands is evident, i.e., cuboidal neck cells, followed by mid-region mucous neck cells, and chief cells at the base with parietal cells scattered throughout the gland, but predominantly in the mid-gland regions (Fig. 7).

In the pyloric region parietal and chief cells are absent. Typically only one cell type is evident, a mucus-secreting cell similar to the mucous neck cells of the fundic region (Fig. 8). Pyloric glands are highly coiled and possess wide foveolae (Fig. 8).

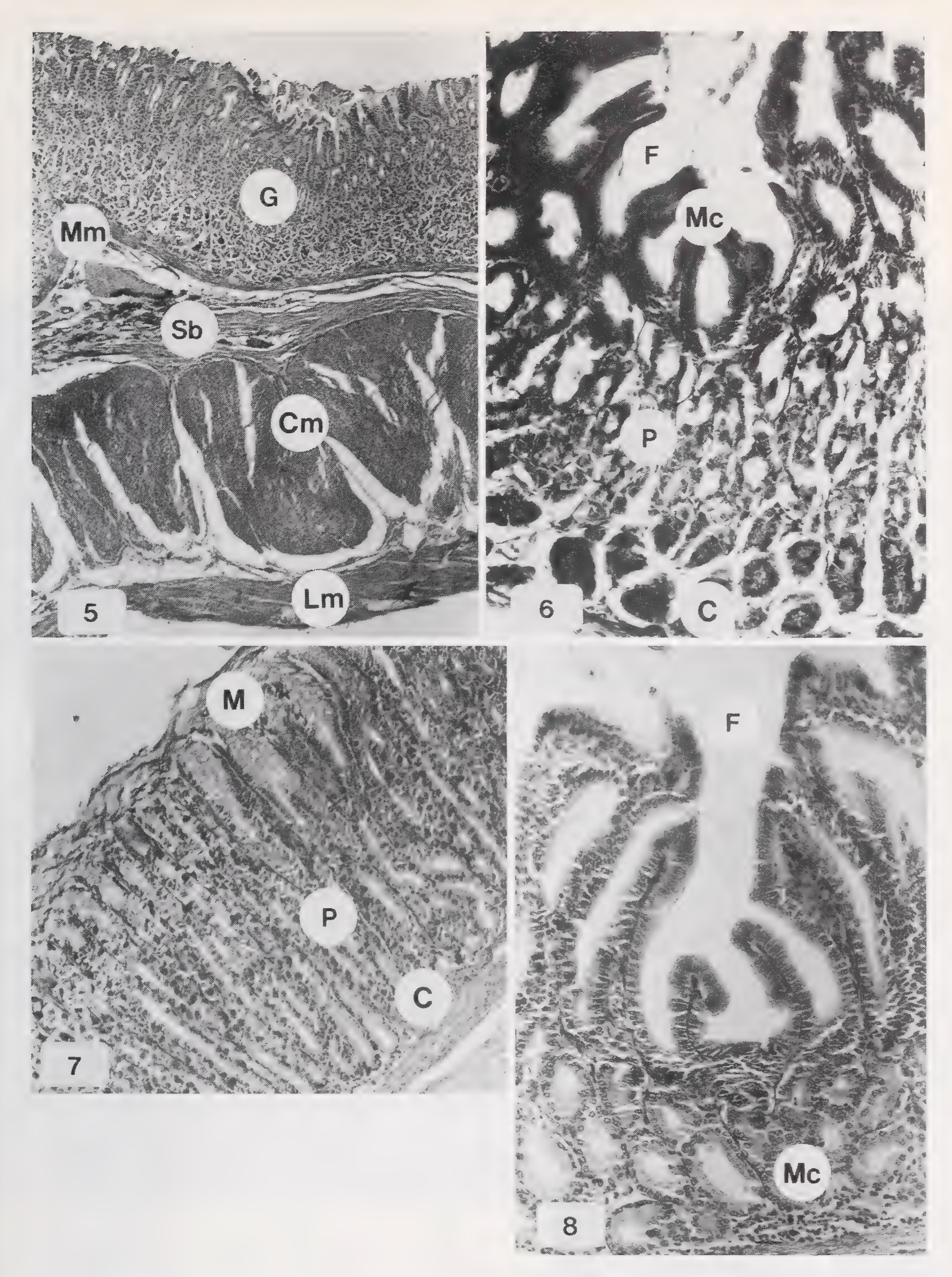


Fig. 5. A typical mammalian gastric tissue plan was observed. G = glandular tissue, Mm = muscularis mucosa, Sb = submucosa, Cm = circular muscle layer, Lm = longitudinal muscle layer. – *Fig. 6.* A section of the cardiac glands showing mucoid neck cells (Mc), parietal cells (P) and chief cells (C). F = foveolum of gland. – *Fig. 7.* A photograph of a section of fundic glands showing the long, tubular nature of the glands. M = mucus, P = region of parietal cells, C = region of chief cells. – *Fig. 8.* A photograph of a pyloric gland. F = foveolum of gland, Mc = mucus-secreting cells

Caecum

The caecum also possesses a typical mammalian alimentary tissue plan (Fig. 9). The muscularis externa is continuous with that of the ileum and the proximal colon; the submucosa of loose connective tissue maintains a constant thickness throughout the caecum (Fig. 9). The muscularis mucosae is continuous with that of the ileum and colon. A lamina propria of fine connective tissue and elastin fibres is present above the muscularis mucosae and extends between the glandular tissue (Fig. 9).

The surface epithelium consists of predominantly columnar absorptive cells, and numerous crypts with wide openings that extend along the length of the caecum. These glands contain numerous columnar mucous goblet cells (Fig. 10).

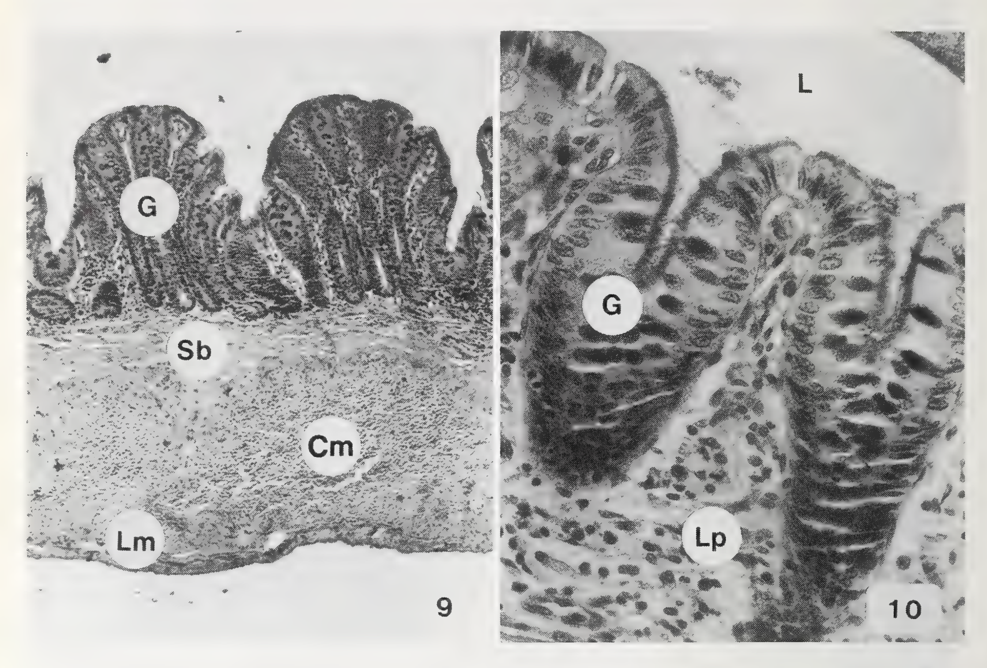


Fig. 9. A photograph showing the typical mammalian alimentary tissue plan of the caecum. G = glandular region, Sb = submucosa, Cm = circular muscle layer, Lm = longitudinal muscle layer. – *Fig. 10.* A photograph of two caecal crypts, showing the abundance of goblet cells (G) and the lamina propria (Lp) between the crypts

Histologically, no differences are apparent between the ampulla and corpus caeci, or between juvenile and adult caeca.

Electron microscopy

Stomach

Material examined by SEM was limited to fundic and pyloric tissue. The pyloric region of the stomach is characterised by deep infoldings (Fig. 11). The pyloric glands open into these recesses and the columnar epithelial cells show a typical "cobblestone" surface appearance (Fig. 11).

Numerous sessile filamentous bacteria in palisade configuration were present in the adult fundus (Fig. 12), while in the juvenile few isolated pockets of shorter bacteria were found (Fig. 13). No bacteria were present in the pars pylorica of either monkey.

Caecum

SEM observations support the light-microscopic findings. The surfaces of both the corpus caeci and ampulla caeci contain numerous crypts and a dense covering of long, threadlike microvilli (Figs. 14 and 15). TEM sections through the caecal crypts show that the crypts are surrounded by tall columnar epithelial and numerous goblet cells (Fig. 16). The nuclei of the goblet cells are basally situated and numerous supranuclear mitochondria are present.

Large numbers of cocco-bacilli and cocci occur, apparently unattached, among the

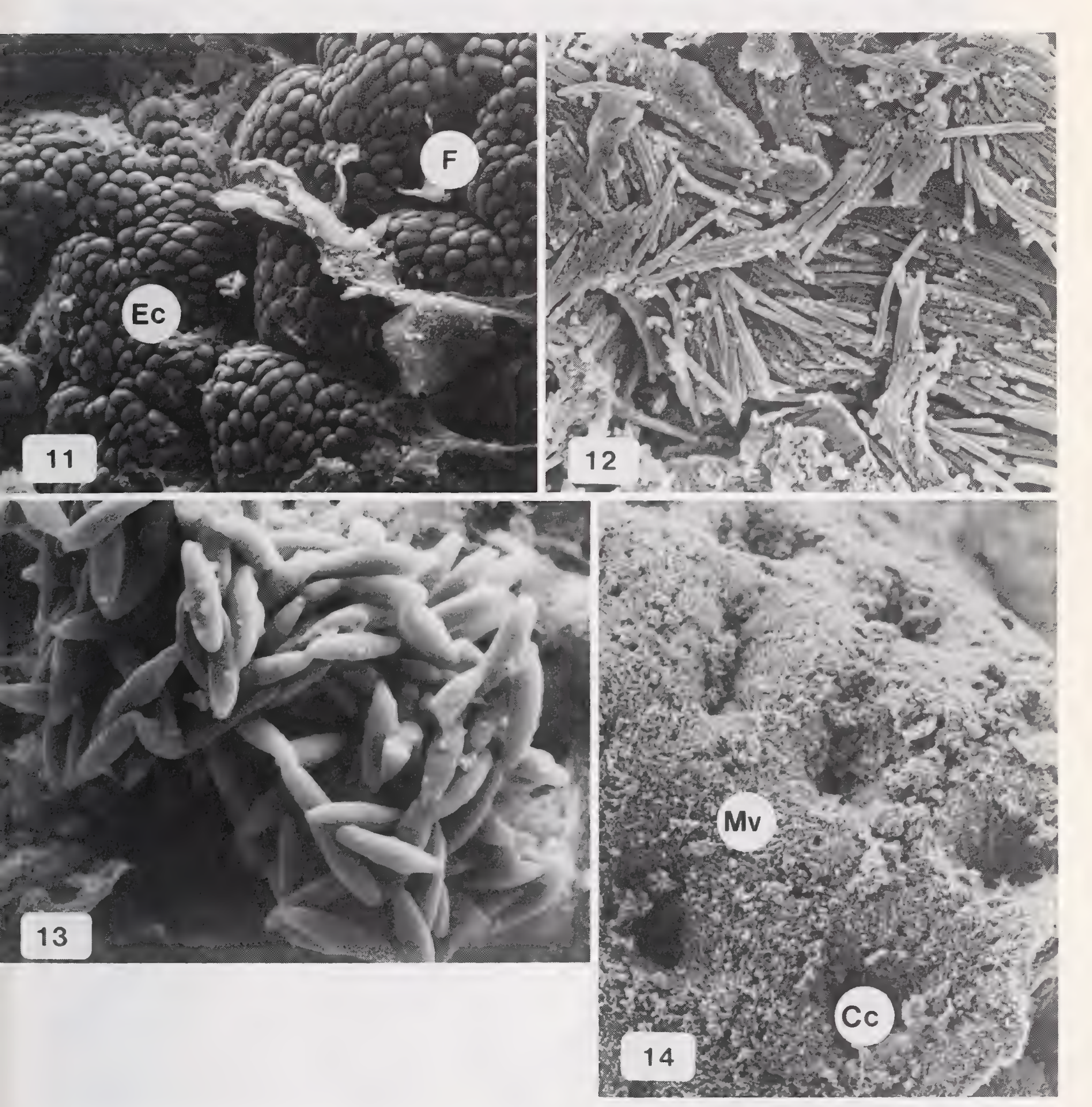


Fig. 11. A scanning electron micrograph of two pyloric glands, showing the foveola of the glands (F) and the typical cobblestone appearance of epithelial cell surfaces (Ec). – *Fig. 12.* Bacilli in the fundus of adult *C. m. erythrarchus*. – *Fig. 13.* Cocco-bacilli in the fundus of juvenile *C. m. erythrarchus*. – *Fig. 14.* A micrograph of the caecal epithelial surface showing the dense layer of microvilli (Mv) and the caecal crypts (Cc)

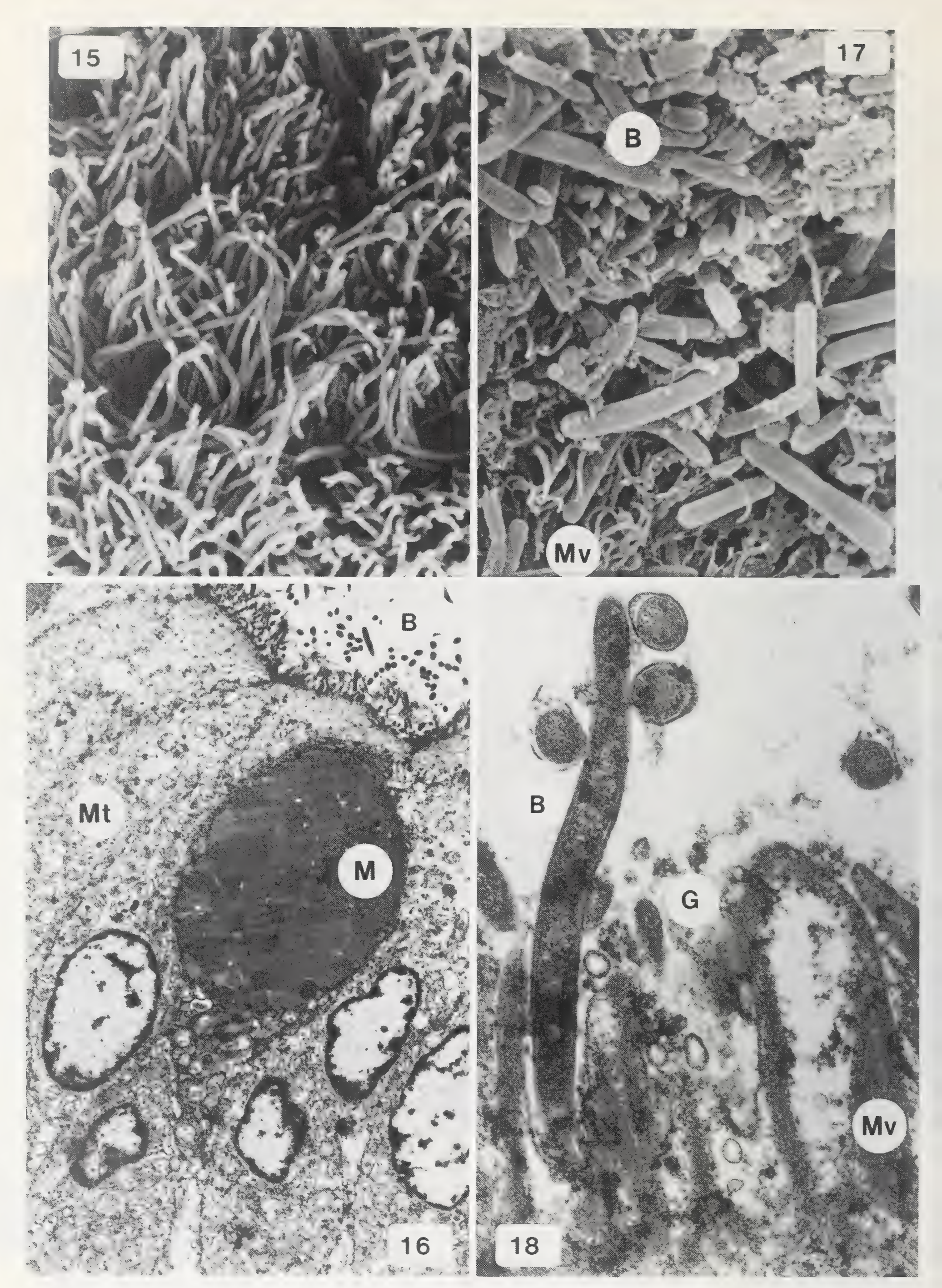


Fig. 15. A high-power micrograph of caecal microvilli. – *Fig. 16*. A transmission electron micrograph of a section through a caecal crypt, showing bacteria (B) in the crypt lumen and the mucoid body (M) of a goblet cell. Mt = mitochondria. – *Fig. 17*. A micrograph showing bacteria (B) on the caecal surface. Mv = microvilli. – *Fig. 18*. A micrograph showing the close association of a bacterium (B) with the microvilli (Mv). G = glycocalyx

mucus and food particles on the caecal surface (Fig. 17) and also penetrate into the caecal crypts. Under TEM the close association of the bacteria in the crypt lumen with the microvillar border is striking (Fig. 18). Many of the bacteria are lodged between the microvilli and appear to indent the apical plasma membrane of the cells (Fig. 19), but no bacterial penetration of cells is evident.

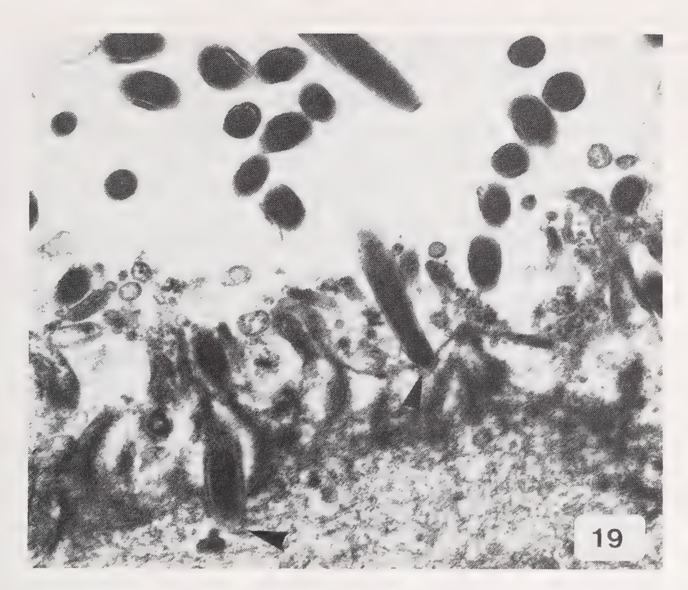


Fig. 19. Bacteria in the lumen of a caecal crypt. Some bacteria indent the plasma membrane (arrows)

Discussion

The food sources of primates can be classified into three major groups, depending on their structure and biochemical composition, and resulting digestibility (Chivers and Hladik 1980). These are fruits, leaves and animal matter. "Fruits" include unripe (e.g. flowers) and ripe (fleshy) parts, seeds and tubers, i.e., mostly the reproductive parts of plants, which are foods containing short-chain sugars that are hydrolyzed rapidly for absorption and immediate use. "Leaves" include young and mature leaves, grasses, stems and also barks and gums, i.e., the vegetative parts of plants, which are foods usually containing protein and long-chain sugars that require fermentation in an enlarged stomach or large intestine. "Animal matter" includes invertebrates and small vertebrates, which provide sources of protein and fat that are easily digested and, therefore, require a relatively short and simple gut (Chivers and Hladik 1980).

C. m. erythrarchus has the following percentage volumetric dietary composition for 713 plant food items scored in the Cape Vidal dune forest: fruits 69.2 %; leaves 23.6 %; animal matter 4.8 %; other 1.6 % (Lawes 1986, unpubl. data). Thus, the Samango is a typical frugivore (Chivers and Hladik 1980), subsisting predominantly on fruits and supplementing the diet with varying amounts of leaves and insects. Fruits are easily digested and absorbed, while leaves require a fermentation process if a maximal energy return from the foliar component of the diet is to be achieved (Milton 1981). From a knowledge of the diet and the gastric anatomy of the stomach and caecum of *C. m. erythrarchus,* it is possible to speculate on the digestive and foraging strategy used by the animal and whether a fermentation process is likely in the gut.

Stomach

The stomach of *C. m. erythrarchus* is a simple glandular unilocular sac, typical of the subfamily Cercopithecinae (Hill 1958; Langer 1985). In the stomach three main glandular areas of the mucosa, the cardiac, fundic and pyloric regions, are identified. The gastric

secretions of proteolytic enzymes, hydrochloric acid and mucus are associated with these three areas of the stomach (Langer 1985).

The well-developed gastric muscle layers and numerous rugae of the adult may facilitate mechanical digestion (the mixing, grinding and soaking of digesta) and provide a greater surface area for secretion, respectively, possibly as a result of the greater nutritoinal demand of the adult monkey. The primarily frugivorous diet of the Samango, however, does not require much mechanical breakdown in the stomach. The last premolars of frugivores tend to become molariform to provide additional crushing and grinding surfaces (Maier 1984), while the cusps and edges of the molars of the Samango are bunodont (low and blunt). Thus, foods can be masticated to such a degree as to allow the maximum surface area for digestion, and the function of the rugae in the adult may simply be to provide a greater surface area for the production and release of gastric secretions.

Bacteria were present in both adult and juvenile Samango stomachs. It is highly unlikely, however, that the presence of small numbers of bacteria in the unilocular (ancestral, unspecialized; Carleton 1973) stomach is indicative of a fermentation process (Maddock 1981). Where microbial fermentation occurs in the stomach, a voluminous fermentation vat is differentiated, holding food for fermentation and slowing the transit of digesta through the stomach (Langer 1984b). The wholly glandular unilocular stomach of *C. m. erythrarchus* is obviously not suited to this function, since there is no physical or physiological separation of digestive processes in the fore and hindstomach. This is supported by the variable but high pH, as a decline to a low pH would destroy any bacteria present.

The stomach of *C. m. erythrarchus,* therefore, likely functions in the initial digestion of the high energy, easily digestible soluble carbohydrate and protein component of the diet. It is highly unlikely that any bacterial cellulolytic fermentation occurs, and although some initial gastric digestion of the foliar component may occur in the stomach, fermentative breakdown of leaves must surely occur elsewhere in the gut.

Caecum

No multicellular animal is known to synthesise cellulase and in consequence the animal is deprived not only of the nutrient value of the cellulose itself, but also of the digestible cell contents bounded by the cellulose wall (Janis 1976). Therefore a great advantage can be gained by an animal that can include fibrous components in its diet by entering into a symbiotic association with cellulase-producing bacteria, but it must provide a fermentation chamber within the digestive tract where these bacteria can digest the cellulose (Janis 1976).

The importance of the caecum and colon in fermentation processes has been determined for many herbivorous mammals (Currier et al. 1960; Johnson and Mcbee 1967; Yang et al. 1968; Mckenzie 1978; Snipes 1978, 1979; Clemens and Phillips 1980; Clemens and Maloiy 1981; Van Hoven et al. 1981; Snipes 1981, 1982a, b, 1984a, b). It is possible that the caecum of *C. m. erythrarchus* functions as a fermentation chamber for the breakdown of the protein and fibre-rich leaf component of the diet, and evidence for this speculation is delivered in the investigation.

The major products of the fermentation of carbohydrates are usually the volatile fatty acids (VFAs), acetic, propionic and butyric (and methane). Fermentative activity is usually measured by determining VFA concentration in a portion of the alimentary tract (Parra 1978). The presence of these organic acids along the digestive tract of non-ruminant herbivores has been demonstrated in vivo repeatedly (Rerat 1978); their concentrations are very large and reach a maximum at the level of the caecum and colon. Studies on four species of African Cercopithecinae have confirmed this distribution of VFAs along the digestive tract (Clemens and Phillips 1980; Clemens and Maloiy 1981). The concen-

tration of organic acids in the stomach is low, with lactic acid representing over half the total amount. Their concentration remains low in the small intestine but increases abruptly in the caecum and proximal half of the colon, where the passage of digesta is probably slowed down greatly by the taeniae and haustra (Clemens and Phillips 1980; Clemens and Maloiy 1981). The high concentrations of VFAs are strong evidence for an extensive microbial fermentation in the caecum and colon of these four primate species.

Microbial fermantation within the digestive tract of primates is a relatively new concept (Clemens and Phillips 1980). With the exception of the Colobinae with their complex foreguts (Bauchop and Martucci 1968; Ohwaki et al. 1974), it was believed until recently that primates were generally incapable of fermenting and digesting complex carbohydrates. However, the concentration of organic acids produced in the caecum and colon of the baboon, Sykes monkey, Vervet monkey and bushbaby (Clemens and Phillips 1980; Clemens and Maloiy 1981) are comparable to those observed in the foregut of ruminants and the hindguts of dogs, pigs and ponies (Swenson 1982).

Considerable numbers of bacteria (representing a large biomass) are present in the caecum of *C. m. erythrarchus* and the close association of many bacteria with the epithelium is striking. In the Koala *(Phascolarctos cinereus)* the close association of bacteria with the epithelium aids absorption by epithelial cells of the products of microbial fermentation (Mckenzie 1978). In the Samango, an actual penetration of bacteria into the epithelium is not evident, as was characteristic in the Koala. Rather, the adherence of the bacteria to the epithelium is in the form of an intermicrovillar location of the bacteria. Together with the large numbers of bacteria found among food particles, the presence of the adhering bacteria suggests that the caecum and microflora function symbiotically as a fermentation vat.

In *C. m. erythrarchus* the pH values along sections of the gastrointestinal tract are very similar to those recorded for two congeneric primate species, *C. mitis* and *C. pygerythrus* (Clemens and Phillips 1980; Clemens and Maloiy 1981). High concentrations of VFAs were present in the caeca of these two species, leading to a lowering of the pH. Due to the similar pH values along the GIT of all three species and the fact that high concentrations of VFA's have been observed in *C. mitis* and *C. pygerythrus,* it seems likely that the low pH in the caecum of *C. m. erythrarchus* is a result of the presence of high concentrations of VFAs. These acids are formed as breakdown products of microbial fermentation; this evidence, together with the observed large biomass of bacteria, also suggests that the caecum functions as a fermentation chamber. These aspects of physiology are to be investigated in *C. m. erythrarchus.*

The close proximity of ileocaecal and caecocolical orifices has been observed in previous studies (Snipes 1981, 1982a, b). This is interpreted as providing the possibility of a rapid transport of intestinal contents directly from ileum to colon, thereby by-passing the greater portion of the caecum (Snipes 1982b). This probably occurs with protein-rich, fibre-poor foodstuffs. Protein-poor and fibre-rich foodstuffs, however, require long-term fermentation activity for the necessary breakdown of cellulose, which would occur in the body of the caecum under optimal fermentation conditions (Snipes 1982b). The presence of extensive musculature in the ileocaecal junction of *C. m. erythrarchus,* which appears to act as a valve/sphincter, could aid this directional flow, thereby enabling optimal fermentation conditions to persist in the caecum.

The possible significance of caecal and colonic taeniae and resulting huastra has been discussed by Gabella (1982 op. cit. Snipes 1982b, 1984a). He implies that the condensation of the longitudinal muscle into narrow bands (taeniae) may represent a specialization allowing mixing and movement of contents, as would be favourable for a "fermentation-vat" function of the caecum. Haustra are interpreted as advantageous for the fermentation process, acting as areas for slowing the rate of passage of digesta and thus allowing the process of fermentation to occur in a more suitable environment (Langer 1979; Clemens

and Phillips 1980; Langer 1984a). The possession of well developed taeniae and haustra along the caecum and colon again strongly suggests active fermentation in these regions.

The striking structural differences between adult and juvenile caeca may be attributable to the fermentation process. The adult possesses a relatively small caecum with numerous folds and a large, haustrated colon, while the juvenile has a large caecum and a relatively small colon. In the adult, although caecal fermentation almost certainly occurs, colonic fermentation may be more important to the monkey. In the juvenile the colon has not developed to adult size and the caecum is proportionately larger and possibly more important in the fermentation process. Johnson and McBee (1967) state that caecal fermentation in the porcupine *(Erethizon dorsatum epixanthrum)* appears to be of increasing importance in larger, older animals, and that this could be offset by younger animals having a proportionately larger caecum (Johnson and McBee 1967).

Four major facts exemplify the importance of hindgut fermentation as an energy source in *C. m. erythrarchus*:

1. The presence of taeniae and haustra in the caecum and colon.
2. The resulting slow rate of passage of digesta (Gabella 1981 op. cit Langer 1979; Snipes 1984a).
3. The presence of numerous bacteria interspersed within the microvilli.
4. The high VFA concentrations in congeneric species with similar anatomies and pH values.

However, the extent of the fermentation process in the caecum and colon of *C. m. erythrarchus* is not known at present and is the subject of further investigation.

Conclusion

It is possible to interpret the morphology of the stomach and caecum of *C. m. erythrarchus* in terms of the dietary requirements of the animal. The Samango eats primarily fruit (Lawes 1986 unpub. data), which is generally rich in nonstructural carbohydrates but low in protein. The simple, glandular stomach provides copious secretions of acids and enzymes necessary for the breakdown of the high quality and easily digestible fruit component, with consequent high utilisation of the nonstructural, soluble carbohydrates. However, the Samango supplements its primarily frugivorous diet with a considerable amount of foliar material (23.6 % of dietary composition). Leaves are high in protein and structural carbohydrates, and to maximize energy returns from leaves requires slow passage rates of food for microbial fermentation to occur. The convoluted caecum and capacious colon of the Samango both possess taeniae and haustra, which slow down the passage rate of food and suggest that an active fermentation process occurs. This ensures maximal energy returns from the foliar component of the diet and from undigested fruit pectins. The caecal and colonic fermentation would be particularly important in mid-winter when food quality and abundance is low, and Samango's experience a "crunch" period with a relatively nutrient-poor diet.

Acknowledgements

We would like to thank Mr. M. J. Lawes and Mr. R. Ferguson for their help in collecting the specimens, and Mr. Lawes for allowing us free access to data collected from his Cape Vidal study area. Our thanks are extended to the staff of the Pietermaritzburg University Electron Microscope Unit for their technical assistance and to Mr. A. H. Maddock for constructive and stimulating discussions.

Zusammenfassung

Die Anatomie von Magen und Blinddarm der Diadem-Meerkatze
Cercopithecus mitis erythrarchus Peters, 1852

Eine Untersuchung der Magen- und Blinddarm-Anatomie von *Cercopithecus mitis erythrarchus* zeigte einen einfachen Drüsenmagen. Der einhöhlige Magen ist für die cercopithecinen Primaten typisch. Blinddarm und Dickdarm sind mit gut entwickelten Tänien und Haustren ausgestattet, die einen Lebensraum für viele symbiontische Bakterien darstellen. Die morphologischen Eigentümlichkeiten werden funktionell in Zusammenhang mit den Verdauungsprozessen dieses hauptsächlich fruchtfressenden Primaten interpretiert.

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Z. Säugetierkunde 53 (1988) 225–234

ISSN 0044-3468

Structure de l'espace et retour au nid chez la gerbille de Mongolie *(Meriones unguiculatus)*

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Reception du Ms. 5. 3. 1987

Abstract

Space utilization and homing in the Mongolian gerbil (Meriones unguiculatus)

The retrieving performance of two groups of ten different Mongolian gerbil adult females and the spontaneous homing performance of the pups were tested under two different conditions of environment from parturition to weaning. The first environment (long cages) was a very long cage (120 × 15 cm), with a closed nesting box. The second (standard cages) was a traditional square rearing-cage (40 × 40 cm), with an open nest. Latencies of first mother-pup contact during the tests under the two conditions did not differ significantly. Retrieval rate was higher from Day 06 to Day 18 in the long cages than in the standard cages. High retrieval rate was noted over a longer period of time in the long cages than in the standard cages. The reverse was the case for spontaneous homing, which made its appearance on Day 10 in the long cages and on Day 02 in the standard cages. These behavioural differences were related to the difference in structure of the available space which might be classified as a "breeding site" and an "extra-nest environment". These experiments show the adaptability of the adult female's behaviour to particular environmental design, which, in natural environments, may be of considerable value for the survival of the pups.

Introduction

Chez de nombreuses espèces de rongeurs, le succès reproducteur est directement lié aux relations comportementales qui s'établissent entre parents et enfants, en particulier durant la période d'allaitement, en raison du caractère nidicole de la plupart de ces jeunes. Le ramassage des jeunes (retrieving des auteurs anglo-saxons) est une de ces relations comportementales dont la manifestation est fortement dépendante de l'espèce étudiée. Le comportement de ramassage a été décrit chez la plupart des rongeurs nidicoles, à l'exception des Dipodidae (genre *Jaculus*), chez qui cette activité ne semble pas exister (Bernard 1969).

L'activité de ramassage s'observe lorsque des jeunes ont quitté le nid ou en ont été retirés expérimentalement. Le jeune est ramené au nid par l'un ou l'autre des parents qui le tient à la gueule. Au fur et à mesure du développement de ses capacités locomotrices, le jeune retourne lui-même au nid. Cette activité peut être interprétée comme une relation comportementale manifeste entre les parents et leurs jeunes. Il peut aussi signifier que l'espace accessible à ces animaux, même dans les conditions de la captivité, n'est pas homogène et isotrope mais présente des qualités locales favorisant la pratique d'un certain type d'activité. Le comportement de ramassage des jeunes peut alors être envisagé comme l'expression d'une structuration, par les animaux, de l'espace disponible pour leurs comportements. Dans cette optique de structuration spatiale non aléatoire des activités, l'espace peut être divisé en une zone «favorable à l'élevage des jeunes» (c'est à dire, le nid *sensu stricto*) et une zone «non favorable à l'élevage des jeunes», cette dernière pouvant être exposée à des conditions climatiques néfastes ou à l'influence de prédateurs. Les jeunes en bas âge, n'ayant pas de régulation thermique efficace, se refroidissent dès qu'ils sont hors du nid. Cet inconfort thermique se traduit par des émissions d'ultra-sons chez *M.*

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unguiculatus (De Ghett 1974). Dans ce cas, cette division est attestée par le fait qu'au lieu de se coucher sur les jeunes pour les réchauffer au contact de leur corps, les parents les ramènent systématiquement dans le nid.

Chez certaines espèces, comme *Mus musculus* (Noirot 1969), *Baiomys* (Blair 1941), *Peromyscus* (Dudley 1974), *Microtus* (Hatfield 1935), le comportement de ramassage est partagé par les deux parents. Chez d'autres espèces, le ramassage des jeunes est davantage le fait de l'un des parents seulement. Chez *Mesocricetus auratus* (Marques et Valenstein 1976), les mâles adultes effectuent plus fréquemment cette activité que les femelles. Au contraire, chez *Meriones unguiculatus,* c'est presque exclusivement la femelle adulte qui effectue le ramassage des jeunes (ElWood 1975; Waring et Perper 1979). Cette activité ne représente chez les mâles de cette espèce que 0,09 % de leur activité totale dans la période qui s'étend de la naissance au sevrage (Elwood 1975).

Selon Waring et Perper (1979), la fréquence de ramassage évolue de la naissance au sevrage, passant par un maximum cinq jours après la naissance, elle décroit par la suite et s'achève au 18ème jour *post-partum*. L'évolution de ce comportement semble dépendre de variations de la réactivité de la femelle jusqu'au dixième jour *post partum*, et serait liée, par la suite, à l'évolution des capacités motrices et de l'aptitude des jeunes à trouver eux-mêmes le chemin du nid.

Nous avons essayé d'aller au delà de cette explication, en testant l'effet de la structure du site de nidification, d'une part sur l'intensité du ramassage et d'autre part sur la durée d'expression de ce comportement de ramassage tout au long de la période d'allaitement.

Dans son environnement naturel, la gerbille de Mongolie élève ses jeunes dans un terrier sombre et profond, le nid est ainsi très nettement séparé du reste de l'espace où évolue l'animal. Dans le terrier, la pente de la galerie réduit les possibilités de divagation des jeunes (Bannikov 1954).

Les cages classiques de laboratoire utilisées aussi bien par Waring et Perper (1979) que par nous-mêmes, sont des enceintes carrées, de matière plastique, exposées à la lumière artificielle, où le nid et le reste de la cage forment un continuum spatial.

Waring et Perper (1979) ont montré que, dans cette situation expérimentale, le comportement de ramassage évolue en relation avec l'état du milieu intérieur de la femelle, avec la maturation et la mise en place des aptitudes locomotrices des jeunes. Nous avons envisagé l'hypothèse que l'expression du comportement de ramassage dépend aussi de la structure de l'espace disponible pour l'activité des animaux.

Matériel et méthodes

Afin de tester cette hypothèse, nous avons utilisé deux types d'enceintes expérimentales qui différaient par les variables suivantes:
– La forme générale: cage longue et étroite dans un cas, cage carrée dans l'autre cas.
– les caractéristiques physiques de l'environnement du nid: suivant les cas, le nid était situé:
1. Soit dans un espace restreint susceptible de fournir une intense stimulation tactile, où l'éclairage était réduit, rappelant les conditions du nid souterrain, et dans lequel l'entassement peut augmenter les stimulus olfactifs liés au nid (longues cages).
2. Soit dans des cages bien éclairées, avec des nids ouverts (cages standard).
Dans ce dernier cas, le nid n'est pas séparé physiquement du reste de l'enceinte d'élevage, alors que dans l'autre cas, une cloison séparait l'espace de nidification du reste de la cage. Ainsi, la structure de l'espace imposait aux gerbilles adultes une spécialisation pour la réalisation de leurs activités: entretien du nid et périodes de repos dans la boite-nichoir, activité locomotrice, alimentation et prise de boisson dans le reste de la cage.

Longues cages

Longues cages étroites (L × l × h = 150 × 15 × 40 cm), sol en bois, paroi vitrée le long d'un grand côté, grillage sur l'un des petits côtés (fig. 1). A l'autre extrémité, une boite-nichoir de 15 × 15 cm communiquait avec la cage par un orifice de 4 cm de diamètre. Cette boite-nichoir était munie d'une

porte extérieure accessible à l'expérimentateur. La mangeoire et l'abreuvoir étaient situés dans la partie oppossée de la cage. Le jour de la naissance, les adultes, leur portée et les matériaux constituant leur nid usuel étaient placés dans la boite-nichoir.

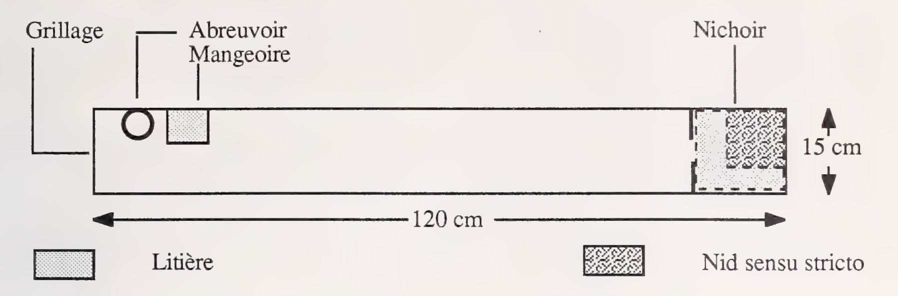


Fig. 1. Longue cage (L. C.)

Cages standard

Il s'agissait de cages standard d'élevage (40 × 40 × 15 cm) fermées par un couvercle supérieur de barreaux d'acier (fig. 2). Comme usuel, la nourriture et le biberon étaient inclus dans le couvercle. Le fond de la cage était couvert de sciure de bois. Les nids étaient toujours construits dans un angle de la cage, avec des débris de papier.

Dans les deux types de cage, les animaux disposaient de feuilles de papier-ouate destiné à être déchiqueté et à complèter la construction du nid.

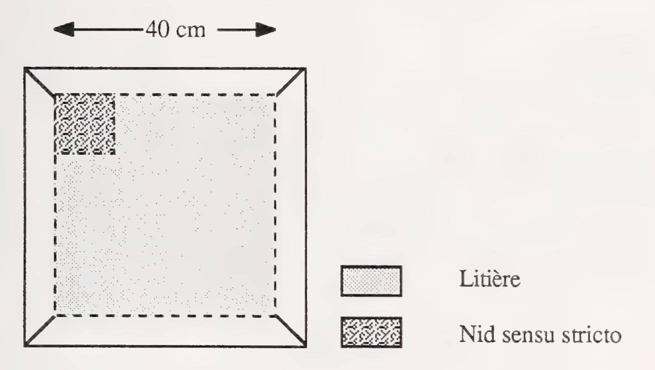


Fig. 2. Cage standard (C. S.)

Sujets d'expérience

Les couples reproducteurs utilisés dans cette expérience provenaient de l'élevage du laboratoire d'Ethologie. Ils étaient élevés comme couples permanents. Dix couples différents et leurs portées ont été utilisés dans ce protocole, pour chaque type de boite. Le nombre médian de jeunes par portée était de cinq. La parité médiane des femelles était de deux aussi bien pour la série des longues cages que pour les cages standard, avec quatre femelles primipares dans chaque condition.

Conditions d'élevage

Dans les deux types de cage, la température ambiante était de 22 ± 2 °C. Un cycle automatique d'éclairage (14 heures de jour/10 heures de nuit) allumait la lumière à 7 heures du matin. La nourriture (sous forme d'aliments compressés UAR A03) ainsi que l'eau de boisson étaient disponibles en permanence *ad libitum*. Une fois par semaine, des graines de tournesol étaient distribuées.

Protocole expérimental

Le jour de la parturition constitue le jour J00. Les tests sont effectués quotidiennement de J01 à J19, entre 11.00 et 12.00 heures. Une cage de chaque type est testée en alternance. Juste avant le test, les parents sont enlevés de la cage. Trois jeunes, pris au hasard, sont enlevés du nid et placés sur le plancher de la cage, à trente centimètres du nid. La femelle adulte est alors introduite dans la cage par la partie la plus éloignée du nid. Le moment d'introduction de la femelle est le temps T0 de la période d'observation qui dure dix minutes. Nous enregistrons les évènements suivants (ainsi que les moments et durées de ces activités):

- premier contact entre la mère et l'un des jeunes;
- premier, second et troisième acte de ramassage (c'est à dire moment où la femelle ayant ainsi le jeune dans la gueule commence à le transporter; les échecs d'une tentative de transport vers le nid ne sont pas pris en compte);
- premier, second et troisième retours spontanés des jeunes dans le nid, le cas échéant, avant la fin des dix minutes;
- les jeunes qui n'ont pas été ramassés ou qui n'ont pas regagné le nid par leur propres moyens sont considérés comme «restant hors du nid».

Traitements statistiques

La comparaison, entre les deux conditions, du nombre total de jeunes ramassés, du nombre total de jeunes rentrant spontanément au nid, ou de jeunes non ramassés a été réalisée à l'aide de tests de KHI carré (d.d.l. = 1; $p < 0.05$), ou à l'aide de tests de Fisher, lorsque nécessaire. La comparaison des mesures temporelles a été faite par des tests U de Mann-Whitney bidirectionnels à $p < 0.05$.

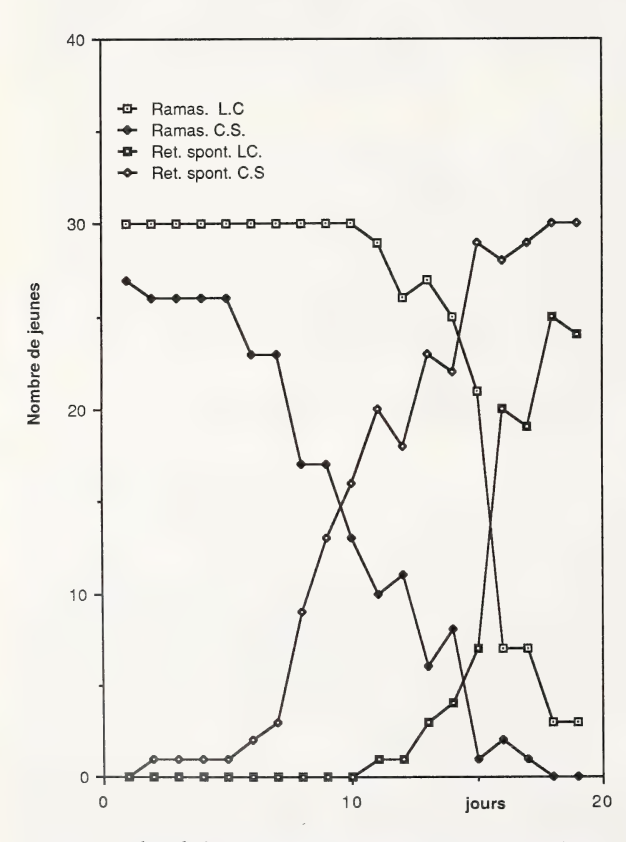


Fig. 3. Nombre de jeunes ramassés ou retournant spontanément au nid, en fonction de leur âge

Résultats

L'analyse des enregistrements nous a fourni des informations sur l'évolution quantitative du ramassage des jeunes par les femelles, sur le retour spontané des jeunes, sur les contacts mère–jeunes et sur les jeunes «restant hors du nid», de J01 à J19.

L'activité de ramassage

Dans les conditions décrites ci-dessus, nous avons pu distinguer, au cours de la période d'élevage, trois phases (fig. 3). La première phase se caractérise par une fréquence élevée de l'activité de ramassage. Celle-ci diminue au cours de la deuxième phase et disparait dans la troisième phase. La première phase se prolonge jusqu'au jour J10 dans les longues cages, et s'arrête au jour J05 dans les cages standard.

Dans les longues cages, tous les jeunes sont ramassés

de J01 à J10. Dans les cages standard, les plus forts pourcentages de ramassage ont été de 90 % le jour J01 et de 86 % de J02 à J05. La deuxième phase s'est étendue de J12 à J17 dans les longues cages et de J06 à J14 dans les cages standard.

Les fréquences de ramassage sont significativement plus élevées dans les longues cages que dans les cages standard, entre J06 et J15 (les différences étant significatives pendant chacun de ces 10 jours avec une probabilité d'au moins $p<0.05$). Dans les cages standard, seulement 50 % des jeunes sont ramassés par la mère à partir du jour J09, tandis qu'il a fallu attendre le jour J16 pour obtenir un score aussi faible dans les longues cages.

L'évolution de cette activité présente alors une diminution rapide dans les longues cages, tandis que, dans les cages standard, la diminution est régulière et sa pente plus faible.

La fréquence cumulée des femelles qui n'ont pas ramassé leur trois jeunes dans les deux conditions ne se superpose à aucun moment (fig. 4). Il s'ensuit que ces conditions diffèrent significativement. Le ramassage complet s'observe sur une plus longue période dans les longues cages que dans les cages standard.

Dans les longues cages, le nombre médian de jeunes non ramassés par portée a été nul avant le jour J16, puis de trois. Dans les cages standard, le nombre médian par portée de jeunes non ramassées a été de un à J14, de 2 à J17 et de 3 à J18.

Latence de ramassage

Cette variable représente le temps qui sépare le premier contact mère–jeune du ramassage du premier jeune (fig. 5). Des analyses de variance de Friedman faites sur ces données ont montré qu'il y avait une modification dans les latences du premier ramassage quand les 10 premiers jours d'expérimentation (c'est à dire quand toutes les femelles sauf une ramassent au moins un jeune) sont pris en compte ($Xr = 34.9$ avec d. d. l. = 9 dans les longues cages et $Xr = 27.4$ avec d. d. l. = 8 dans les cages standard).

Afin de comparer nos résultats à ceux de Waring et Perper, nous avons comparé les latences de ramassage à J01 à celles de J04, puis les latences de J04 à celles de J12. Des tests de Wilcoxon montrent qu'il y a une diminution significative entre J01 et J04 (Wilcoxon $t = 0$ pour les longues cages et $t = 1$ pour les cages standard, $p < 0.05$) et une augmentation des latences de J04 à J12 ($t = 7$ pour les longues cages et $t = 0$ pour les cages standard, $p < 0.05$). Les latences n'ont été significativement plus élevées dans les cages standard que dans les longues cages que les jours J10 et J11. Cependant, au jour J01, cette latence était significativement plus élevée dans les longues cages que dans les cages standard (Mann Whitney: $U = 11$, $n1 = 10$, $n2 = 9$, $p<0.01$).

Durée de ramassage

C'est l'intervalle de temps nécessaire pour effectuer le ramassage de trois jeunes. Cette variable fait intervenir les temps de transport, mais aussi les pauses observées par la femelle, entre le premier et le dernier ramassage. Cette durée est plus longue dans les longues cages que dans les cages standard, avec une différence significative à J06 ($U = 22, 5$, $n1 = n2 = 9$, $p<0.05$).

Le retour spontané

Le retour des jeunes dans leurs nids, par leurs propres moyens, a été observé dès le jour J01 pour les longues cages, mais seulement au jour J11 pour les cages standard. Une forte fréquence de retour spontané s'observe à partir de J11 dans les cages standard, mais seulement à partir de J16 dans les longues cages. Les fréquences de retour spontané ont été significativement plus élevées dans les cages standard que dans les longues cages, de J08 à J18 (avec des probabilités au moins égales à $p < 0.05$).

La fig. 3 montre la proportion cumulée de portées dans lesquelles au moins un jeune a regagné le nid par ses propres moyens.

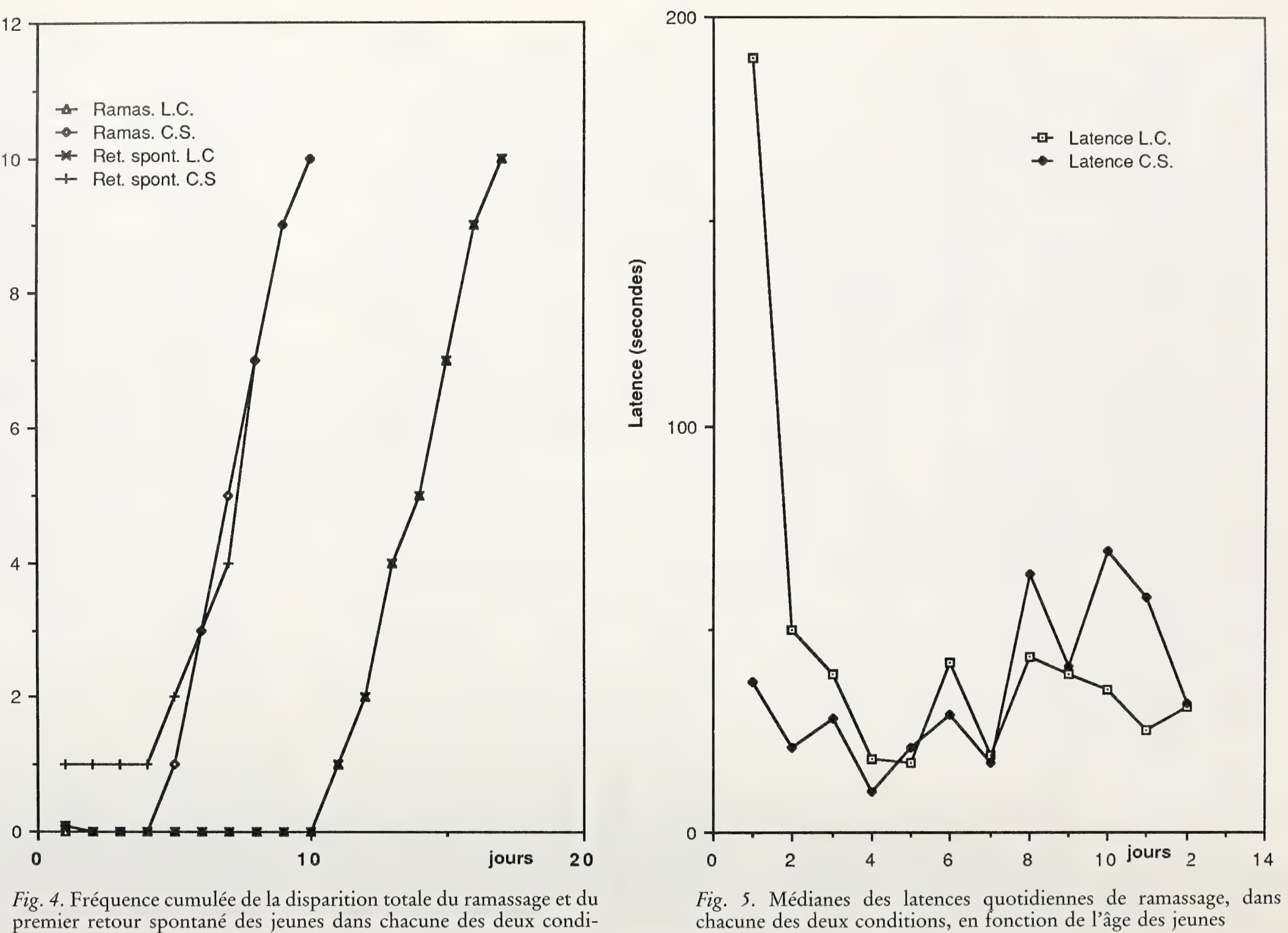


Fig. 4. Fréquence cumulée de la disparition totale du ramassage et du premier retour spontané des jeunes dans chacune des deux conditions.

Fig. 5. Médianes des latences quotidiennes de ramassage, dans chacune des deux conditions, en fonction de l'âge des jeunes

Dans les longues cages, le nombre médian de jeunes qui regagnent le nid par leurs propres moyens a été nul jusqu'à J10, et de 3 par portée à partir de J16.

Dans les cages standard, ce nombre a augmenté régulièrement, passant de 1 pour J08, à 2 pour J10 et 3 pour J13. Des différences significatives dans le nombre de jeunes réussissant le retour au nid ont été observées entre les deux conditions (avec $p < 0.05$ au moins) entre J08 et J18.

Dans les longues cages, la fréquence de retour au nid a été d'emblée forte, tandis que dans les cages standard, elle s'élevait progressivement.

Il faut rappeler, parmi les étapes de la maturation organo-génétique, que si l'aptitude locomotrice des jeunes gerbilles est notable dès J2, l'ouverture des yeux n'intervient que vers J16–J17, ce qui modifie fortement les capacités d'orientation des jeunes dans l'espace, et en particulier leur aptitude à localiser le nid.

Les jeunes restant sur place

Dans les longues cages, la totalité des jeunes a été remassée par la femelle jusqu'au jour J10.

Dans les cages standard, le nombre de jeunes restant sur place est passé de 10 % à J01 à 16 % à J08. Après cette période, le nombre de ces jeunes est demeuré proche de zéro, tandis que dans les longues cages, il augmentait. Cependant, aucune différence significative n'a été trouvée entre les deux conditions.

Discussion

Des différences s'observent entre les deux conditions en ce qui concerne les fréquences de comportement de ramassage, les taux de retour spontané et les taux de jeunes non ramassés. L'origine génétique commune des animaux utilisés dans cette expérience nous amène à inférer les causes de ces différences à la structure de l'environnement mis à la disposition des animaux.

L'expression du comportement de ramassage se caractérise, chez la gerbille de Mongolie, par une évolution au cours des dix neuf premiers jours de la vie du jeune. Cette évolution peut être divisée en trois phases, distinguées par les fréquences de ramassage. Ceci avait été décrit par Waring et Perper (1979); notre expérimentation a permis de montrer qu'en plus de l'influence de facteurs physiologiques, un effet modulateur des conditions environnementales peut s'ajouter. En effet, dans notre situation expérimentale, les taux de ramassage des jeunes ont toujours été plus élevés dans les longues cages à nid bien séparé que dans les cages standard de laboratoire. De plus, dans les longues cages, le comportement de ramassage s'exprime plus longtemps au cours de l'ontogénèse des jeunes que dans les cages standard. Les différences de performances observées entre les deux conditions, le premier jour du test, peuvent être rapportées au fait que dans les longues cages, les gerbilles adultes et leurs portées sont placées dans la cage de test la veille de la première manipulation, tandis que les animaux des cages standard continuent de vivre dans leur cage familière.

Les différences entre les deux conditions se sont avérées significatives essentiellement durant la période où le taux de ramassage était particulièrement élevé. Cette période a été plus longue dans les longues cages que dans les cages standard.

Contrairement a Waring et Perper (1979), nous n'avons pas observé de phase initiale de croissance du taux de ramassage des jeunes, pendant les quatre premiers jours. Dans notre situation expérimentale, l'expression du ramassage s'est révélée forte d'emblée, dès le début de la période d'allaitement. La seule différence significative porte sur la diminution de la latence de ramassage entre J01 et J04–05, suivie d'une augmentation de ce paramètre, jusqu'à la fin de notre expérimentation, dans les deux conditions expérimentales.

Comme Waring et Perper (1979) l'avaient noté, l'intensité des émissions ultra-sonores, qui décroit après J03 (De Ghett 1974) n'est pas le seul paramètre qui explique la décroissance du taux de ramassage que ces auteurs ont observé après J03.

Dans la situation expérimentale que nous avons utilisé, le ramassage s'est exprimé pendant une période plus longue dans les longues cages que dans les cages standard. Aucun élément, bibliographique ou d'observation, ne nous permet d'envisager une évolution différentielle tant des émissions ultra-sonores que de la thermorégulation dans chacune de ces deux conditions. Selon MacManus (1971), les jeunes gerbilles ont une régulation de type ectothermique avant J12 et deviennent progressivement endothermiques entre J12 et J20, moment du sevrage. Comme les deux catégories de cages se trouvaient à la même température ambiante, l'hypothèse d'une chute de température plus importante chez les jeunes de l'une des conditions ne peut être retenue.

Le retour spontané des jeunes au nid s'observe plus tôt dans les cages ordinaires que dans les grandes cages. Dans les premières, la maturation musculaire permet souvent aux jeunes de rejoindre le nid avant même que la femelle adulte ne puisse établir un premier contact avec eux.

Aucun élément ne peut permettre de penser que la maturation musculaire puisse être différente dans les deux situations expérimentales.

De ce fait, force nous est de rapporter les différences observées aux différences inhérentes aux deux conditions, et, en particulier, aux différences d'organisation de l'espace.

L'activité de ramassage ne commence que lorsque la femelle a perçu l'absence des jeunes du nid. Quoique la distance à laquelle les expérimentateurs plaçaient les jeunes au moment du test était la même dans les deux conditions, les femelles adultes réagissaient avec une latence plus longue au stimulus «jeune» placé dans la zone «extérieure au nid» dans les longues cages que dans les cages standard.

Nos résultats peuvent être interprétés comme l'indice d'une meilleure perception, par les femelles, des limites entre ces deux zones (entre le «nid» et le «reste de la cage») dans les longues cages. Dans les cages standard, au contraire, on peut penser que l'ensemble de la cage est perçu comme une extension de la zone de nidification avec laquelle elle constitue un continuum spatial. Dans cet ordre d'idée, nous pensons que les longues cages constituent un modèle expérimental qui recrée des conditions de vie plus proches de celles de l'environnement naturel de la gerbille de Mongolie que les cages classiques de laboratoire.

Le fait que, dans les grandes cages, l'âge auquel les jeunes arrivent à se rendre seuls au nid est plus tardif que dans les cages carrées s'explique par le mode de locomotion des jeunes.

Dans les longues cages, les retours spontanés au nid ne deviennent vraiment fréquents qu'après l'ouverture des yeux, qui a lieu vers le seizième jour en moyenne, dans notre élevage.

L'observation montre qu'avant cet âge, le retour au nid est le résultat d'une locomotion paraissant non-orientée. La probabilité de succès de ce type de locomotion est, évidemment, plus forte dans une cage carrée ordinaire puisque, dans la majorité des cas, les déplacement des jeunes se font, dans les deux conditions, en suivant, tactilement, les parois de la cage. Ce comportement est lié, selon certains, à un thigmotactisme; mais il peut s'agir, aussi bien, du maintien d'un contact sensoriel supplémentaire chez un animal qui dispose de peu de moyens d'orientation. Les parois des cages standard ont un périmètre de 160 centimètres, les longues cages, un périmètre de 270 centimètres. Quelle que soit la direction de marche, dans les cages carrées, le jeune aboutira au nid. Il n'en est pas de même dans les longues cages où une orientation en sens inverse de la direction du nid provoquera un temps de retour au nid très long (en cas de réorientation) ou l'absence de retour. Il est notable que, dans cette condition, le retour spontané ne dépasse 50 % qu'après l'ouverture des yeux. Ceci fait penser à une certaine inefficacité d'un repérage tactile dans la régulation

de cette activité. L'olfaction ne semble pas intervenir dans la localisation du nid pendant la période étudiée ici (Yahr et al. 1983), et ce n'est qu'après l'ouverture des yeux que les performances des jeunes dans les grandes cages s'améliorent.

Les performances de ramassage des jeunes et de leur retour spontané que nous avons observées dans les longues cages sont exactement inversement corrélées. Il existe donc une concordance entre le comportement de ramassage de la femelle et l'inaptitude des jeunes à rentrer au nid. Ceci est confirmé par l'observation d'une persistance du comportement de ramassage de la femelle pendant une période allant jusqu'à 48 jours, lorsque les jeunes d'une femelle sont remplacés périodiquement par d'autres jeunes plus immatures (Pourtier L., comm. pers.).

L'inaptitude des jeunes pour le retour spontané dans un type d'environnement relativement complexe constitue un handicap vis à vis des chances de survie, dans un environnement naturel. Celui-ci est contre-balancé par le plus fort taux de ramassage des femelles dans cette situation. Ces expériences montrent le caractère adaptatif du comportement de la femelle, dont l'expression différentielle, en fonction des caractéristiques de l'espace, peut se révéler d'une considérable valeur pour la survie des jeunes.

Résumé

Les auteurs ont testé les performances de ramassage des jeunes dans deux groupes composés chacun de dix Gerbilles de Mongolie femelles adultes ainsi que celles de retour spontané au nid de leurs jeunes, dans deux environnements expérimentaux différents, de la parturition au sevrage. Le premier environnement consistait en une très longue cage (120 × 15 cm), munie d'une boite nichoir. Le second était une cage standard, carrée (40 × 40 cm), avec un nid ouvert. Les latences du premier contact femelle-jeune durant les tests ne diffèrent pas significativement. Le taux de ramassage des jeunes est plus élevé entre les jours 6 et 18 *post-partum* pour les animaux des longues cages que pour ceux des cages standard. De forts taux de ramassage sont observés pendant une plus longue période dans les longues cages que dans les cages standard. L'inverse est observé en ce qui concerne le retour spontané des jeunes au nid, qui fait son apparition au dixième jour dans les longues cages et au deuxième jour dans les cages standard. Ces différences comportementales sont rapportées aux différences de structures des deux environnements expérimentaux accessibles aux animaux, permettant de distinguer une zone «favorable à l'élevage des jeunes» et une zone «non favorable à l'élevage des jeunes». Ce protocole a permis de montrer les possibilités d'adaptation du comportement de la femelle adulte à la structuration particulière de son environnement, ce qui, dans un environnement naturel est décisif pour la survie des jeunes.

Zusammenfassung

Raumnutzung und Rückkehr zum Nest bei der Mongolischen Rennmaus (Meriones unguiculatus)

Geprüft wurde in zwei verschiedenen Käfigtypen an je 10 Weibchen von *Meriones unguiculatus,* mit welcher Intensität sie ihre Jungen im Alter von 1–19 Tagen ins Nest trugen und wie weit die Jungen aktiv zum Nest zurückkehrten. Käfig A war gestreckt (120 × 15 cm) und enthielt einen geschlossenen Nestkasten. Käfig B war quadratisch und mit einem offenen Nest ausgestattet.

In Käfig A wurden die Jungen intensiver eingetragen als in Käfig B. Dafür kehrten in Käfig B die jungen häufiger aktiv ins Nest zurück als in Käfig A. Diese Unterschiede können damit erklärt werden, daß Käfigtyp A deutlicher in eine Nest- und eine Außenregion gegliedert war und die Jungen bei Orientierung an der Käfigwand mit dem Tastsinn in Käfig B eher zufällig auf das Nest stießen als in Käfig A.

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Z. Säugetierkunde 53 (1988) 235–244

ISSN 0044-3468

The effect of fire on the small mammal community in Hluhluwe Game Reserve

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Receipt of Ms. 15. 1. 1987

Abstract

Investigated was the effect of fire on small mammals. Four permanent trapping grids in *Acacia* savanna, subjected to various burning treatments, were monitored from July 1982 to December 1983. An area not burnt and an area with a patchy-burn showed an increase in rodent densities immediately after the fire. A burning experiment disclosed no animals fleeing from the blaze. Species composition and diversity indexes of the small mammal community were relatively unaffected by the burns. No age-class of *Praomys natalensis* was more vulnerable to the fire than any others. Each sex of *P. natalensis* and *Aethomys chrysophilus* responded similarly to the burns while more *Lemniscomys griselda* females were captured in post-burn trapping. An effect of burning was that cleanly burnt areas seemed to stimulate reproduction; relatively more *P. natalensis* adult came into reproductive condition during spring in these areas. The mean distance between captures (range distance) of *P. natalensis* fluctuated inversely with changes in population densities. The mobility of *P. natalensis* and *L. griselda* following the burns increased while the survival rates of *P. natalensis, A. chrysophilus,* and *L. griselda* appeared greater in unburnt areas. The 1982/83 drought caused the population densities of each species in the small mammal community to "crash".

Introduction

In recognition of the vital role fire plays in natural ecosystems, its use has now been accepted as a necessary tool in land management (Edwards 1984). The burning programme employed at Hluhluwe Game Reserve (HGR) has two major objectives, to combat bush encroachment; and to maintain the fire-climax grasslands (unpubl. Natal Parks Board report).

In order to maintain a rich and diverse rodent community correct grassland management in natural areas is vital. The immediate responses of small mammals to a blaze vary; animals may flee from the flames (Delany 1974; Swanepoel 1981), or seek refuge in burrows, holes, crevices, or islands of vegetation missed by fire (Cheeseman and Delany 1979; Begg et al. 1981) while others burn or suffocate (Delany 1974; Christian 1977). Cheeseman and Delany (1979) report rodents moving ahead of the flames (200–300 m), and they suggest the animals respond to a warning stimulus (noise of combustion, smell of/or smoke) other than the heat of the fire itself. Several authors report direct mortality as being negligible because of high post-burn survival (Delany 1974; Begg et al. 1981; Swanepoel 1981).

Small mammal habitat is severely and abruptly modified by fire in that food supply is reduced and cover removed. Post-burn numbers decline due to hunger and enhanced predation (Begg et al. 1981; Swanepoel 1981; Rowe-Rowe and Lowry 1982). Reproduction and recruitment can be affected by fire through delayed breeding and reduced litter sizes (Begg et al. 1981).

The objective of the present study was to investigate the effect of controlled burning on the abundance and diversity of small mammals in HGR.

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Study area

HGR (28° 00′ – 28° 91′S, 32° 00′ – 32° 09′E; Fig. 1) covers 23 067 ha; the topography, characterised by a profusion of drainage lines, is extremely rugged with altitude ranging from 90 m to 750 m a.s.l. The mean annual rainfall (averaged over 52 y) is 968 mm with the wettest months occurring between October and March.

The study area falls within the Zululand Thornveld subcategory of the Coastal Tropical Forest Types, and the Lowveld subcategory of the Tropical Bush and Savanna types of Acocks (1975). Forest communities are restricted from high rainfall hillsides to riverine belts. Much of the area is covered by savannas dominated by *Acacias,* in particular *A. karroo, A. burkei, A. nilotica, A. tortilis, A. gerrardii, A. nigrescens,* and *A. caffra.* These generally have grass cover of tall tufted perennials such as *Themeda triandra* and *Cymbopogon* spp. (Brooks and Macdonald 1983).

Trapping and vegetation monitoring were conducted primarily in *Acacia* savanna in the study area situated in the northeastern corner of HGR (Fig. 1).

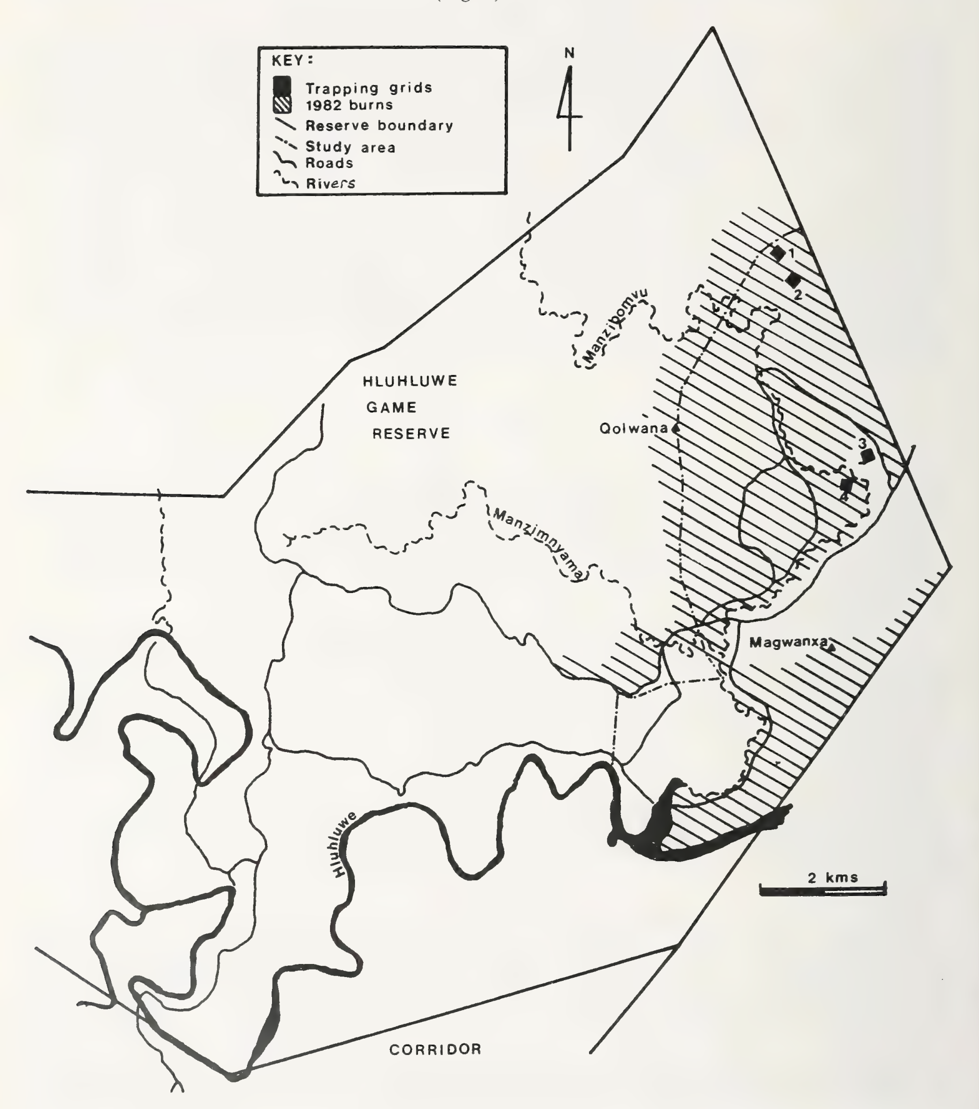


Fig. 1. A map of the 1982 burns in the Hluhluwe Game Reserve study area showing the locations of the trapping grids. 1 = clean-burn 1, 2 = patchy-burn, 3 = no-burn, 4 = clean-burn 2

Materials and methods

Trapping was conducted on 10 × 10 grids with PVC livetraps (WILLAN 1978), set at 15 m intervals. The trap was usually placed in the most likely site within one metre of the trap station; all traps were checked daily in the morning, rebaited, with a mixture of equal parts rolled oats and peanut butter, and reset if necessary.

Captured animals were identified, weighed, and sexed; and capture points on the grid were recorded. The following criteria were used to evaluate reproductive condition: females, the state of the vaginal opening (perforate or imperforate) and the condition of the nipples (small, enlarged, lactating); males, the position of the testes (scrotal or abdominal). Each animal was individually marked using a toe-clip code before release at its capture site.

Animals were assigned to age-classes according to body mass i. e. adult, sub-adult, or juvenile (Table 1). The lower limit of the adult class was calculated by subtracting the standard deviation from the mean weight of the "scrotal" or "perforate adults", to accommodate animals in an emaciated condition caused by the drought. The mean trap distance between captures of individuals was used to assess the range distance of each species.

Table 1. **The weight categories used to determine age classes of four rodent species**

Species	Females adult (g)	Females sub-adult (g)	Females juvenile (g)	Males adult (g)	Males sub-adult (g)	Males juvenile (g)
Praomys natalensis	>33	21–33	<21	>31	21–31	<21
Saccostomus campestris	>36	21–36	<21	>41	21–41	<21
Aethomys chrysophilus	>63	31–63	<31	>71	31–71	<31
Lemniscomys griselda	>47	21–47	<21	>64	21–64	<21

Population densities were estimated by a weighted mean mark-recapture formula (BEGON 1979):

$$\hat{N} = \frac{M_i \times n_i}{(\Sigma m_i + 1)}$$

where $\hat{N}$ = estimate of the population
M_i = number of marked individuals at risk on day i
m_i = number of marked individuals caught on day i
n_i = number of individuals caught on day i

Standard error was calculated with the formula (BEGON 1979):

$$SE = \hat{N} \sqrt{\frac{1}{\Sigma m_i + 1} + \frac{2}{(\Sigma m_i + 1)^2} + \frac{6}{(\Sigma m_i + 1)^3}}$$

Species diversity was calculated using the formula (SHANNON 1948):

$$H = \frac{n \log n - f_i \log f_i}{n}$$

where H = species diversity index, f_i = number of individuals of one species caught during the trapping session, and n = total number of individuals of all species caught during the trapping session (SHANNON 1948). Diversity indexes were compared with the test devised by HUTCHESON (1970).

After extensive exploratory trapping in the study area, four permanent grids were sited in *Acacia* savanna which had not been burnt since 1980. The grids were loosely paired i. e. about 600 m distant, the two pairs were separated by about 3.5 kms (Fig. 1).

Three of the grids were burnt in the first week of August 1982. One had a patchy burn while two had clean burns; the fourth unburnt grid was used as a control. The patchy burn was hot and clean with a mosiac of discrete unburnt islands of the herb layer remaining; these islands varied in area from several to a hundred or more square metres. The clean burns were hot and thorough with no herb layer remaining. In each case the clean-burn grid was adjacent to either the patchy-burn or the no-burn grid. Grids were trapped just before (July) and just after (August) the burns in 1982 and on seven other occasions until December 1983.

During the 1983 burning programme in August two grids were clean-burnt (the patchy-burn grid and its adjacent clean-burn grid). Only pre-burn trapping was conducted as low rodent numbers did not justify a post-burn trapping programme.

Vegetation recovery in clean-burn 1 grid was monitored from August to December 1982. Cover

was subjectively assessed using a replicated (0,5 m^2) quadrat method, which included height measured where the majority of leaves and/or inflorescences ended.

In an experiment to assess the immediate response of small mammals to the blaze, a 10 m wide fire-break was burnt around a 2.7 ha grid. The following day observers were strategically placed along the fire-break before igniting the area, in order to observe and record emigrants.

Results

Population estimates indicate that small mammal responses to the different burning treatments vary. Post-burn density on the no-burn and patchy-burn grids increased while a reduction on both clean-burn grids was evident (Table 2). The anticipated rise in numbers in the summer breeding period was stifled by the drought; population estimates showed a

Table 2. **Total captures, population density estimates, diversity indexes, and trap success determined from the trapping results of four grids monitored from July 1982–Dec. 1983 in Hluhluwe Game Reserve**

Grid	Year	Month	Total captured (n)	Population estimate (animals ha^{-1})	Diversity index	Trap success (%)
Patchy-Burn	1982	Jul	40	14.9	0.3	10.0
		Aug	35	20.9	0.3	8.8
		Sep	19	6.5	0.4	4.8
		Nov	16	6.0	0.6	4.0
	1983	Feb	8	2.6	0.7	2.0
		Apr	8	2.7	0.3	2.0
		Aug	5	2.0	0.6	1.3
		Oct	3	0.9	0	0.8
		Dec	2	0.2	0.3	0.5
Clean-Burn 1	1982	Jul	92	35.7	0.3	23.0
		Aug	38	13.7	0.2	9.5
		Sep	24	8.8	0.3	6.0
		Nov	14	5.3	0	3.5
	1983	Feb	13	5.3	0.3	3.3
		Apr	5	1.8	0.2	1.3
		Aug	9	2.8	0.3	2.3
		Oct	2	0.6	0	0.5
		Dec	2	0.9	0.3	0.5
No-Burn	1982	Jul	93	34.3	0.3	23.3
		Aug	120	43.5	0.4	30.0
		Sep	84	26.9	0.5	21.0
		Nov	43	13.3	0.5	10.8
	1983	Feb	16	5.9	0.5	4.0
		Apr	15	3.8	0.6	3.8
		Aug	2	0.4	0.3	0.5
		Oct	3	0.4	0.3	0.8
		Dec	2	0	0	0.5
Clean-Burn 2	1982	Jul	54	22.0	0.1	13.5
		Aug	49	18.6	0.1	12.3
		Sep	30	11.0	0	7.5
		Nov	14	4.4	0.2	3.5
	1983	Feb	10	2.6	0.1	2.5
		Apr	6	1.8	0	1.5
		Aug	5	2.6	0.5	1.3
		Oct	3	0.6	0.3	0.8
		Dec	4	1.8	0	1.0

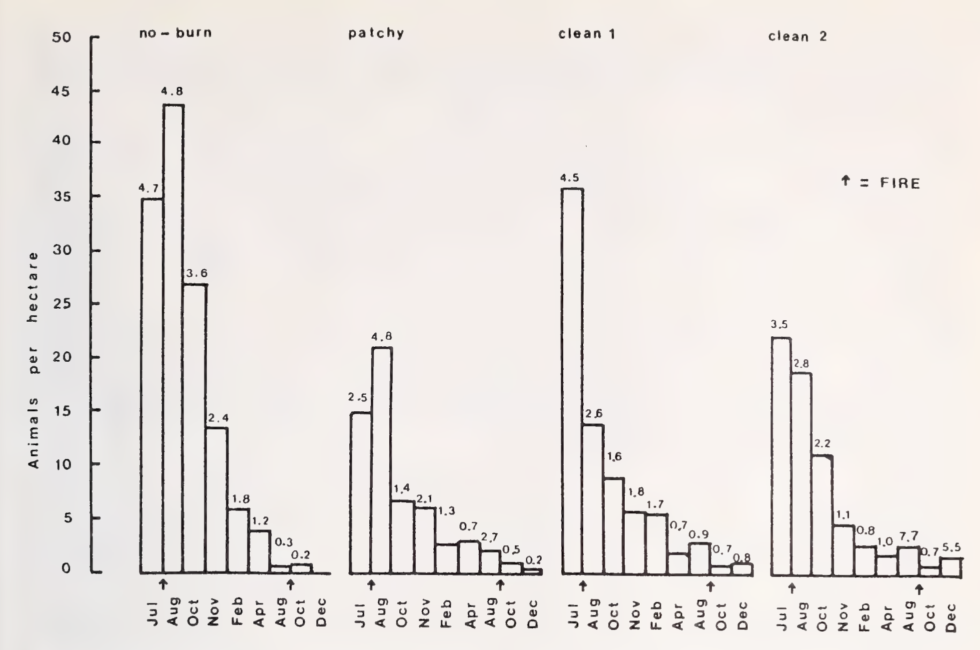


Fig. 2. Population estimates on the variously treated (burnt) grids from Jul 1982 to Dec 1983, standard error given above each histogram

steady decline on all grids to the end of 1983, with marginal increases in the clean-burn grids in December (Fig. 2).

Contingency tables indicated that there were no significant changes in species composition after the burns except on the no-burn grid (Table 3). The diversity index of the small mammal community in each burning treatment did not change significantly ($p > 0.2$–0.5) immediately after the fire but subsequent changes showed that the no-burn and patchy-burn grids maintained a more diverse community than the clean-burn grids (Table 2).

To determine which age-class of *P. natalensis,* if any, was susceptible to the blaze, pre-

Table 3. **Pre- and post-burn species composition in each burning treatment area (1982)**
Contingency tables ($2 \times \varkappa$) are used to determine whether significant changes in the community as a result of fire had occurred

Species	No-burn pre-	No-burn post-	Clean-burn 2 pre-	Clean-burn 2 post-	Patchy-burn pre-	Patchy-burn post-	Clean-burn 1 pre-	Clean-burn 1 post-
P. natalensis	69	81	53	47	33	29	76	33
L. griselda	3	21	0	2	2	3	11	3
A. chrysophilus	4	3	–	–	1	2	1	–
S. campestris	–	–	–	–	–	1	–	–
M. minutoides	–	1	–	–	–	–	–	–
S. pratensis	–	–	–	–	–	–	1	–
C. hirta	17	14	1	–	4	–	3	2
Total caught	93	120	54	49	40	35	92	38
χ^2	11.51		0.45		2.27		0.47	
d.f.	3		1		3		2	
p =	<0.01 *		>0.5		>0.2		>0.2	

* significant

Table 4. Mean range distance estimates with standard errors (SE), of four rodent species in Hluhluwe Game Reserve from July 1982 to April 1983
Differences between male and female distances are tested for significance (Student's t)

Species	n	Females distance (m)	SE	n	Males distance (m)	SE	n	Combined distance (m)	SE	t	df	p
P. natalensis	128	27.6	1.6	155	26.6	1.8	283	27.1	1.2	0.53	281	>0.5
S. campestris	1	15.0	–	1	33.5	–	2	24.3	–	–	–	–
A. chrysophilus	18	24.5	2.4	13	21.8	2.6	31	23.3	1.8	0.74	29	>0.4
L. griselda	8	19.5	3.7	19	23.0	3.5	27	22.0	2.7	0.59	25	>0.9

and post-burn comparisons were made of each grid after establishing that the age-structure in each grid did not differ significantly from the overall age-structure. A null hypothesis that the two sets of attributes, i. e. age-structure and the grid areas selected for different burning treatments, were independent of each other was upheld ($\varkappa^2 = 2.89$, $p > 0.8$). However, pre- and post-burn age structures of *P. natalensis* showed a significant difference in the clean-burn 2 treatment only, where the juvenile catch increased ($p < 0.05$).

Pre- and post-burn sex ratios showed no significant differences for *P. natalensis* ($\varkappa^2 = 0.004$, df = 1, $p > 0.99$), *A. chrysophilus* ($\varkappa^2 = 0.03$, df = 1, $p > 0.9$) and *L. griselda* ($\varkappa^2 = 2.68$, df = 1, $p > 0.1$). The pre- and post-burn inter-grid sex ratios of *P. natalensis* showed no significant differences ($\varkappa^2 = 0.0004$, df = 1, $p > 0.99$).

The range distance for each species is given in Table 4, *P. natalensis* appears to have a marginally greater range than *Saccostomus campestris, A. chrysophilus,* or *L. griselda.* Small sample sizes precluded inter-treatment analysis of range distances in all species but *P. natalensis.* Pre- and post-burn range distance fluctuations vary inversely with changes in population density estimates (Table 5).

A high percentage of pre-burn marked *P. natalensis* (75.8 and 68.1 %) and *L. griselda* (66.7 %) were caught during post-burn trapping on the clean-burn grids, while in the no-burn grid the number of pre-burn marked *P. natalensis* was relatively lower at 56.8 % with only 24.1 % of the catch in the patchy-burn grid bearing pre-burn marks. The survival rate for *P. natalensis, A. chrysophilus,* and *L. griselda* was highest in the no-burn treatment (Table 6).

The ratio of breeding to non-breeding *P. natalensis* decreased until November (July 1:7.1, August 1:9.7, September 1:12.5) when there was an upsurge in breeding condition and the ratio changed to 1:0.5. Analysis shows that the inter-treatment ratios vary considerably (Table 7).

The recovery of vegetation cover/height is depicted in Fig. 3; despite improved habitat conditions small mammal numbers showed a temporal decline.

Rainfall during the study period was well below average, the effect of fire, therefore, could only be investigated in the short term, i. e. before the drought had established itself.

The experiment planned to assess the small mammal response to the blaze gave no indication of animals fleeing from the flames; one of the 35 animals known to be in the area fled across the firebreak. Quinn (1979) reported burnt and unburnt carcasses of small mammals found after fires in chaparral shrubs, while Tevis (1956) actually witnessed animals perishing in the flames. Only one unburnt carcass *(L. griselda)* was found after the fire in the experiment during the present study.

Table 5. **Changes in pre- and post-burn population densities and mean range distances [with standard errors (SE) and a test for significance (Student's t)] of *P. natalensis* in each burning treatment**

Treatment	Population density estimates (animals/ha)		Mean range distance (m)						
	pre-burn	post-burn	pre-burn	SE	post-burn	SE	t	df	p
No-burn	34.3	43.5	26.0	4.3	23.9	2.5	0.46	63	>0.5
Clean 2	22.0	18.6	24.0	3.3	24.8	2.9	0.18	40	>0.5
Patchy	14.9	20.9	20.8	4.3	16.5	1.5	0.91	19	>0.2
Clean 1	35.7	13.7	28.5	3.4	44.6	13.3	1.71	46	<0.1

Table 6. **Survival rate of *P. natalensis, A. chrysophilus,* and *L. griselda* expressed as a percentage of the number of pre-burn marked animals caught in post-burn trapping sessions**

Species	Burning treatment	Number of marked animals	Survival (%)				
			Aug	Sep	Nov	Feb	Apr
P. natalensis	Patchy	32	21.9	6.3	–	–	–
	Clean 1	67	37.3	17.9	9.0	–	–
	No-burn	63	73.0	38.1	19.1	3.2	–
	Clean 2	52	61.5	28.8	5.8	1.9	–
A. chrysophilus	Patchy	1	100.0	–	–	–	–
	Clean 1	1	–	–	–	–	–
	No-burn	3	–	–	33.3	33.3	33.3
	Clean 2	0	–	–	–	–	–
L. griselda	Patchy	2	–	–	–	–	–
	Clean	9	22.2	–	–	–	–
	No-burn	3	100.0	66.7	–	–	–
	Clean 2	0	–	–	–	–	–

Table 7. **The ratio of breeding to non-breeding *P. natalensis* in various burning treatment areas during November 1982**

Treatment	Breeding : Non-breeding		n
No-burn	0.9	1	17
Patchy-burn	1.5	1	5
Clean-burn 1	6.0	1	14
Clean-burn 2	4.0	1	10

Discussion

Factors influencing the rate at which burnt savanna grassland is recolonised by small mammals include behaviour of the animals involved, proximity to refugia (unburnt grassland or forest inhabited during or shortly after the blaze), rate of vegetation recovery and the type of burn. Recolonisation of burnt areas may extend between two and eight or more months and can, subsequently, yield higher small mammal numbers than unburnt areas (Neal 1970; Stewart 1972; Kern 1977; Cheeseman and Delany 1979; Swanepoel 1981; Rowe-Rowe and Lowry 1982). Kern (1977), who examined the effects of annual August burns, estimated 0.62 animals/ha immediately after the fires, 2.16 animals/ha two months later, and 4.17 animals/ha in January when grasses were seeding profusely.

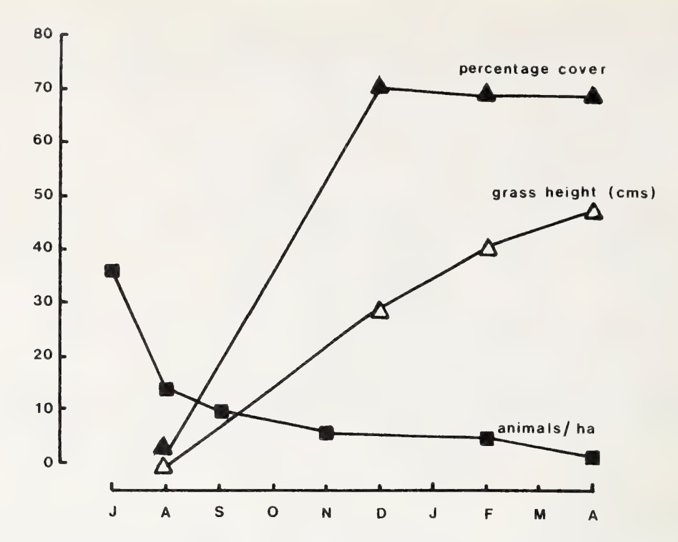


Fig. 3. Recovery of the grass sward (height and percentage cover) after an August clean-burn, related to changes in small mammal numbers, Aug 1982 to Apr 1983

The anticipated small mammal recolonisation of the burnt areas in this study did not occur despite the recovery of the herb layer, the effects of the drought are implicated.

Population estimates

Post-burn population crashes have been recorded by many workers (NEAL 1970; KERN 1977; CHRISTIAN 1977; SWANEPOEL 1981) but pre- and post-burn trapping in the present study suggest that fluctuations in small mammal numbers following fire stem mainly from dispersal. The grids providing cover (no-burn and patchy-burn) showed an increase in numbers whereas the two clean-burn grids, where all cover had been removed, exhibited decreases.

COOK (1959), however, found no evidence that surviving mice emigrated to adjacent unburnt areas, but, most studies (NEAL 1970; CHRISTIAN 1977; KERN 1981; SWANEPOEL 1981) show that migration from the burnt area to an area providing shelter is common.

Species composition

On the no-burn grid, where significant post-burn changes occurred, the number of *P. natalensis* and *L. griselda* were augmented by migrants from the surrounding burnt areas, while the rest of the community remained numerically constant. SWANEPOEL (1981) found that 25 % of *P. natalensis* migrated to an adjacent unburnt area while more mobile *L. griselda* vacated the burnt area completely. On the adjacent clean-burn 2 grid, *P. natalensis* numbers dropped by 11.3 %.

Crocidura hirta disappeared from the patchy-burn grid, while *P. natalensis* numbers increased, and *A. chrysophilus* and *L. griselda* numbers remained constant. The total post-burn captures in this grid decreased yet population estimates increased; the apparent anomaly arose from the high migration rate in this area. First, the *P. natalensis* population had been considerably diluted, only 24.1 % of the post-burn captures bore pre-burn marks compared with 56.8 % in the no-burn grid. Second, increased movement was indicated by the relatively low recapture rate of all marked animals. It is clear that the small mammal community was markedly disrupted by the patchy-burn. In the adjacent clean-

burn 1 grid the poorly represented *A. chrysophilus* disappeared. *C. hirta* numbers remained about constant and *P. natalensis* and *L. griselda* declined noticeably.

Sex ratios

Both sexes of *P. natalensis* reacted alike to the various burning treatments. SWANEPOEL (1981) also reported no significant post-burn changes in sex-ratio of *P. natalensis.* The post-burn sex ratio of *L. griselda,* however, changed noticeably with an increase in number of females caught. The findings of SWANEPOEL (1981) too showed relatively more *L. griselda* females caught after the fire.

Reproduction

CHRISTIAN (1977) found that the effects of fire did not drastically alter the intensity or timing of breeding of deserticolous *Gerbillus paeba* or *Desmodillus auricularis.* BEGG et al. (1981) established that fire affected reproduction and recruitment in all four species in his study area which ranged from closed forest to perennial grasslands. In the present study the difference in breeding to non-breeding ratios of *P. natalensis* in November 1982 on the various burning treatment areas suggested an influence of fire on reproduction; more adults came into reproductive condition on the clean-burn grids.

The reproductive trigger may be low density but DELANY (1972) infers that the onset and termination of breeding could be correlated with biochemical and quantitative changes in diet.

Range distance

CHRISTIAN (1977) has reported that if any critical resources have been destroyed by fire it is likely that survivors on the burnt area would range over greater distances in search of food and cover. The two species studied, *G. paeba* and *D. auricularis,* both had a greater range on the burnt area than on the unburnt area. KERN (1977) also found a slight increase in the home range of *T. leucogaster* on burnt areas.

The range distances on the clean-burn treatments of *P. natalensis* increased after the burns while those on the no- and patchy-burn areas decreased. Though these trends are statistically not significant they do suggest that mobility is probably influenced by an interaction of the effects of fire (sub-optimal habitat, food scarcity) and population densities.

Survival rate

CHRISTIAN (1977) found the survival rate higher, though not significantly so, on the burnt area whereas in the present study the survival of *P. natalensis, A. chrysophilus* and *L. griselda* was higher on the no-burn area. *P. natalensis* showed more resilience in the clean-burn 2 area than the patchy-burn area. Perhaps the intense post-burn disruption and the onset of the drought resulted in the heavy mortality in this area.

The present study showed that the small mammal community is able to cope with the fire itself as numerous aspects (sex ratios, species composition, age structure, diversity) were relatively unaffected. The incidence of fire in the home range of a small mammal is a brief event and only fatal if the animal is engulfed by the flames or asphyxiated by the fumes. Mortality, as a direct result of fire, seems to occur seldomly. The major impact of fire on the small mammal community which leads to marked declines in abundance stems from the sudden and extreme modification of the habitat whereby food supply and cover are removed.

Acknowledgements

We wish to thank Dr P. M. BROOKS for his help in supervising this project. Natal Parks Board and University of Natal staff members willingly provided information and assistance. Numerous field

assistants enabled the successful completion of many arduous tasks in the field. The CSIR, the University of Natal, and the University of Natal/Natal Parks Board Research Fund assisted financially.

Zusammenfassung

Der Einfluß von Bränden auf die Kleinsäuger im Hluhluwe-Wildreservat

Untersucht wurde der Einfluß von Bränden auf die Kleinsäuger. Dazu wurden vom Juli 1982–Dezember 1983 die Kleinsäugerbestände von vier Probeflächen, die vollständig, teilweise oder gar nicht abgebrannt wurden, durch Markierungsfang verfolgt. Auf der nicht und der nur teilweise abgebrannten Fläche stieg die Anzahl der Nager unmittelbar nach dem Brand an. Bei direkter Beobachtung wurden keine vor dem Brand flüchtenden Kleinsäuger festgestellt. Die Artenzusammensetzung und Diversitätsindices blieben nach Bränden relativ unbeeinflußt. Bei *Praomys natalensis* waren die verschiedenen Altersgruppen nicht signifikant verschieden vom Feuer betroffen. Eine Zunahme der Weibchen, die bei *Lemniscomys griselda* nach dem Brand auftrat, war nicht signifikant. Auf völlig abgebrannten Flächen war der Anteil sich fortpflanzender *P. natalensis* erhöht. Die mittlere Aktionsraumgröße nahm bei *P. natalensis* mit zunehmender Dichte ab. Die Überlebensrate der Nager schien auf den nicht abgebrannten Flächen größer zu sein. Eine Dürre in den Jahren 1982/83 führte zu einer allgemeinen Abnahme aller Kleinsäuger des Beobachtungsgebietes in dieser Zeit.

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Z. Säugetierkunde 53 (1988) 245–252

ISSN 0044-3468

Responses of Apennine chamois to human disturbance

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Receipt of Ms. 13. 3. 1987

Abstract

The study measured the effects of human disturbance on the behaviour of different age groups of Apennine chamois *Rupicapra pyrenaica ornata* in three areas with different levels of human presence in the upper Val di Rose, Abruzzo National Park, Italy, in July 1986.

There was no consistent difference in flight distance between the sexes or between grazing and resting animals, in response to standardised experimental approaches, but yearling and sub-adult chamois had significantly shorter flight distances than had young adults. Females with kids had significantly longer flight distances than those without, although the difference was confined to resting animals. Flight distances were least in the area with most visitors and were longest in the most remote area and there was evidence of habituation with repeated exposure to people.

Introduction

The population of chamois *Rupicapra pyrenaica ornata* in the Italian Apennine Mountains numbers fewer than 400 animals, confined to a small area in the Abruzzo National Park, and is described as vulnerable by I.U.C.N. The animals are subject to considerable human disturbance; Cederna and Lovari (1985) showed that the many visitors to the Park (2039 in one study area; 30 days' observation) caused disruption to grazing by forcing the animals to retreat to rock faces. Grazing was completely prevented during the mid-morning peak of tourist activity.

Lovari and Rosto (1985) found that even in the apparent absence of human disturbance, younger, subordinate female chamois grazed at a significantly lower rate and were significantly more vigilant than older, dominant females. Intra-group social rank factors were likely to be involved but it is also possible that human presence might affect the feeding of younger chamois more than that of older ones.

The aims of the present study were: 1. to measure the effects of human disturbance on the behaviour of Apennine chamois of different age and sex, in relation to their previous behaviour (grazing or resting); 2. to compare the responses of animals in different areas of the Abruzzo Park with different amounts of human disturbance; and 3. to find whether chamois would habituate to the continual presence of people.

Study area

The main study areas were in the upper part of the Val di Rose in the Abruzzo National Park (Fig. 1), an area of limestone ridges and alpine meadows at 1850–1942 m altitude. Three areas were used: Passo Cavuto, which was visited very frequently by walkers in summer; Boccanera, which was not used by walkers but where the animals were accustomed to the frequent presence of observers; and Sterpi d'Alto, where the animals were approached less frequently. A few observations were also made on Mt. Amaro, 4 km to the NW, where the animals were less accustomed to people. The study was carried out during July, 1986.

Each of the main study areas supported a largely separate flock of up to 30 chamois, some of which had been ear-tagged for individual recognition in earlier studies.

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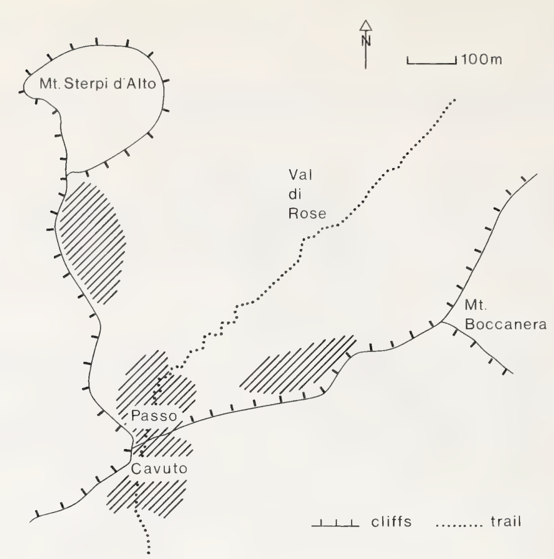


Fig. 1. The main study areas (shaded) in the upper Val di Rose, Abruzzo National Park, L'Aquila, Italy

Material and methods

Animals were allocated to age classes, using the length of their horns in relation to ear length (LOVARI 1985): yearlings had horns around or a little less than the length of their ears; sub-adults (2–3 years old) had horns ¼ – ⅓ longer than the ears; young adults (4–5 years old) had horns 1½ times ear length while adults (over 5 years of age) had horns at least twice the length of the ears. In animals at least two years old, males could be distinguished by their thicker, more strongly curved horns and their penile hair tuft. Yearling males and females were not distinguished.

Some naturally-occurring disturbance of chamois by visitors was observed at close range but such incidents were highly variable in the number of people involved, their direction and speed of approach, whether they were noisy or quiet, etc., so the main study used standardised approaches by the observer. After an initial acclimatisation period of at least 10 min an animal with no others between it and the observer was selected and its sex, age class and activity (grazing or resting) were noted. It was then approached across the slope at a slow walk (0.25 m/s), avoiding any noise or sudden movements. The distance between the animal and the observer was measured with a range-finder whenever there was a change in the chamois' behaviour and the approach was suspended immediately the animal began to move away. The observer then retreated before starting to approach a new animal.

As far as possible, only one approach was made to each animal in a flock on each day, but animals without ear tags were undoubtedly approached on different days, leading to some non-independence in the data and consequent need for caution in the interpretation of statistical tests. Where repeat approaches were carried out on ear-tagged animals, a mean value for each has been used.

Results

Behavioural responses to human approach

In almost all of the 225 approaches made in the main study areas the animals showed the same sequence of behaviour; grazing animals stopped feeding, oriented their heads towards the observer (noted as the alert distance) and moved away, usually with their tails raised (noted as the flight distance); similarly, resting animals oriented and rose to their feet before moving off. Only 3 % omitted orientation of the head before moving. Many (45 %) of the 31 resting animals which were ruminating steadily before being approached continued to do so until they moved off and a further 29 % even continued to ruminate as they moved. Alarm snorts were given in only 4.5 % of approaches.

The changes in the animals' behaviour during approaches tended all to occur within a few seconds, at the same distance from the observer; in only 23 % of approaches did the animal stop activity and orient to the observer at a distance greater than the eventual flight distance. The proportion doing so was, however, significantly higher in resting than in grazing animals and was slightly but not significantly greater in females accompanied by kids than in other adults females (Table 1). In such animals the mean difference between

Table 1. **Percentage of animals with alert distance greater than flight distance**

	N	Grazing Alert	%	N	Resting Alert	%
			Without Kids			
Pass	86	7	8.1	45	18	40.0
Boccanera	23	1	4.3	5	5	100.0
Sterpi d'Alto	34	8	23.5	9	3	33.3
Total	143	16	**11.2**	59	26	**44.1**
	$\chi^2 = 27.42$; $p < 0.001$					
			With Kids			
Pass	3	1		3	1	
Boccanera	6	1		5	4	
Sterpi d'Alto	3	1		3	1	
Total	12	3	**25.0**	11	6	**54.5**
	$\chi^2 = 2.10$; NS					

Overall, 22.7 % with alert distance greater than flight distance.

the alert and flight distances was 1.53 ± 0.15 m (grazing), 2.02 ± 0.25 m (resting) and 3.11 ± 0.56 m in females with kids. (There were no statistically significant differences, however, between these distances.)

Since the majority of animals became alert and then moved away without further approach by the observer, flight distances alone were used in most of the following analyses.

Flight distances in relation to previous activity

This could be compared in nine categories of animal (excluding females with kids); in adult females on Sterpi d'Alto the flight distance was significantly higher in grazing than in resting animals but there was no significant or consistent difference in any of the other groups (Table 2). Marked animals approached both while grazing and while resting also showed no consistent difference in flight distance. Alarm snorts, although uncommon, occurred in 10.2 % of 59 approaches to resting animals but in only 2.1 % of 143 to grazing ones ($\chi^2 = 6.39$; $p < 0.01$). They occurred in a quarter of the eight tests on Mt. Amaro.

Among females accompanied by kids, resting animals had significantly higher flight distances than had grazing ones in the Pass and Boccanera areas (Fig. 2). On Sterpi d'Alto, grazing females with kids had flight distances as long as those of resting ones.

Flight distance in relation to the sex of the animal

This could be compared in only five categories of sub-adult, since the sex of yearlings was not determined and adult males were uncommon in the study area. There was no consistent tendency for one sex to have a greater flight distance (Table 3). Subsequent sections will therefore combine grazing and resting animals of both sexes (excluding females accompanied by kids).

Table 2. **Flight distance in grazing and resting animals**

Age/Sex	Area	Grazing N	Grazing x̄	Grazing SE	Resting N	Resting x̄	Resting SE
Yearlings	Pass	18	**11.8**	0.6	16	10.0	0.7
2–3 yr ♂♂	Pass	20	10.6	0.5	15	**11.8**	1.3
2–3 yr ♂♂	Sterpi	3	**17.3**	2.0	2	14.0	1.0
2–3 yr ♀♀	Pass	9	9.7	0.6	5	**11.8**	0.9
2–3 yr ♀♀	Boccanera	5	13.0	1.9	2	**14.0**	4.0
2–3 yr ♀♀	Sterpi	2	13.3	2.7	3	**14.3**	0.9
4–5 yr ♀♀	Pass	17	**12.8**	0.5	5	11.0	0.7
5+ yr ♀♀	Pass	20	**12.3**	0.5	3	10.5	0.8
5+ yr ♀♀	Sterpi	14	**17.9**	1.2	3	13.7	0.9*

* $t = 2.86$; $p = 0.017$; no other significant differences.

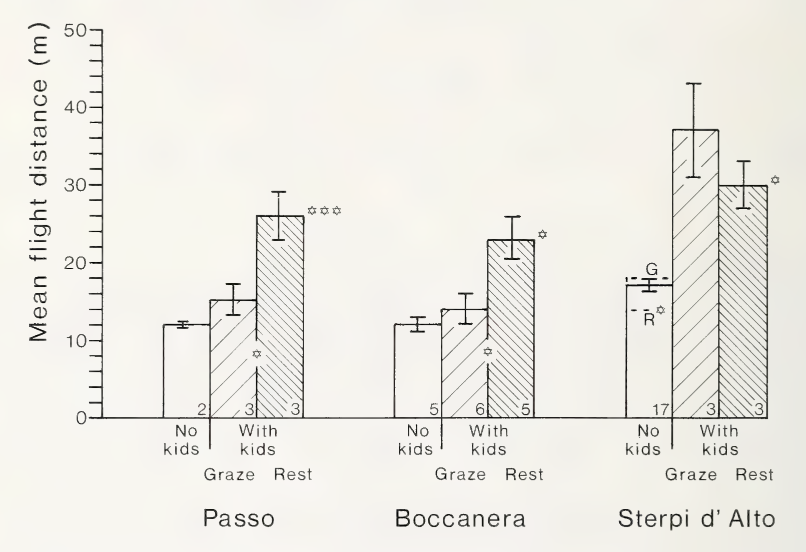


Fig. 2. Flight distances in adult females with and without kids. Asterisks above the columns indicate significant differences from females without kids (* – $p < 0.05$; *** – $p < 0.001$, t tests). Asterisks within columns indicate significant differences between grazing and resting animals ($p < 0.05$, t tests)

Table 3. **Flight distance in male and female sub-adults**

Area	Activity	Male N	Male x̄	Male SE	Female N	Female x̄	Female SE
Pass	grazing	20	**10.6**	0.5	9	9.7	0.6
Pass	resting	15	11.8	1.3	5	11.8	0.9
Boccanera	grazing	2	13.0	1.0	5	13.0	1.9
Sterpi d'Alto	grazing	3	**17.3**	2.0	2	13.3	2.7
Sterpi d'Alto	resting	2	14.0	1.0	3	**14.3**	0.9

No significant differences.

Flight distance in different age classes

Contrary to expectation, young chamois were not more sensitive to disturbance than were older ones – yearlings and sub-adults had slightly but significantly shorter flight distances than had young adults (Fig. 3). Analysis of variance, however, showed no significant variation in flight distance over the four age groups taken together.



Fig. 3. Flight distance in relation to age. Grazing and resting animals of both sexes have been combined, omitting only those with kids. Young adults vs. sub-adults and yearlings, $p < 0.05$ (t tests)

Resting females with kids had longer flight distances than females without kids in all of the three main study areas (Fig. 2). Three ear-tagged females, approached while resting away from their kids, all had shorter flight distances than when resting with their kids.

Flight distance in different areas

In all age groups there was significant variation in mean flight distance between the three main study areas (ANOVA; $p < 0.01$), with the shortest distances in the heavily visited Pass area and the longest in Sterpi d'Alto, where the animals were visited least (Fig. 4). The moderately-studied Boccanera area was intermediate, but young adults there had significantly longer flight distances than those in the Pass area. One marked adult female seen in two areas had a longer flight distance when she was on Sterpi d'Alto than when she was in the Pass. The small number of observations made on Mt. Amaro suggested that flight distances there were about twice those at the Pass (Fig. 4).

Flight distance with repeated approach

When the approaches made to a given sex and age category in each study area were divided into their earlier and later halves, all seven categories with sufficient data showed a shorter flight distance in the second half of the study compared to the first, with significant differences found among yearlings and subadult males (Table 4). Overall, the mean reduction in flight distance was 1.7 m. Six marked animals approached more than once over the study period showed no consistent change in flight distance, but successive approaches were usually at intervals of several days. However, in four animals approached two or three times in quick succession, only two showed a reduction in flight distance while one stayed the same and one showed an increase.

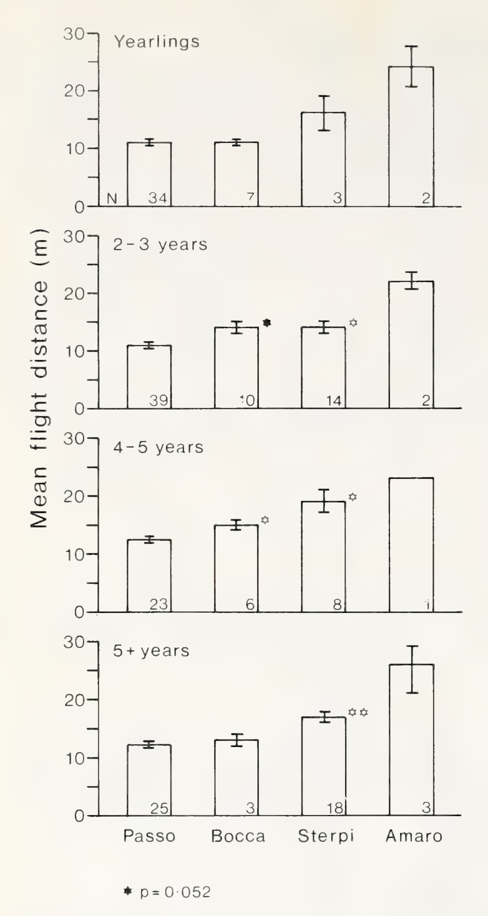


Fig. 4. Flight distance in different study areas; categories of animal as in Fig. 3. Single asterisk indicates significant difference from Pass ($p < 0.05$; t tests); double asterisk indicates significant difference from Pass and Boccanera ($p < 0.01$, t tests)

Discussion

Yearling and sub-adult chamois, although found by LOVARI and ROSTO (1985) to be more vigilant than older ones, did not become alert and flee from a quietly-approaching person at greater distances than did older animals; indeed they allowed significantly closer approach than did young adults. This supports LOVARI and ROSTO's (1985) suggestion that the vigilance of younger animals may be mainly social, with attention directed at other chamois. It is also possible that the animals were looking out for other potential predators such as canids and were not concerned about people. There may also be a higher level of curiosity in younger animals, counteracting fear and leading to their staying longer while being approached.

Resting animals might be expected to have shorter flight distances than grazing ones, which can move away easily, while the resting ones have first to rise to their feet, which might require a higher threshold of fear to be exceeded. However, most chamois showed no difference in flight distance with previous activity, with only adult females on Sterpi d'Alto having significantly shorter flight distances while resting. The opposite was true for females accompanied by kids in the Pass and Boccanera areas. In these, the longer flight distances of resting animals may be related to a greater vulnerability of sitting animals to a sudden rush by predator. This, however, explains only the animals' rising to their feet as a "precautionary" measure, not

Table 4. **Change in flight distance with repeated approach**

Age	Sex	Activity	Area	First half of approaches			Second half of approaches			t	p
				N	$\bar{x}$	SE	N	$\bar{x}$	SE		
1		G	Pass	10	**12.2**	0.9	9	**11.3**	0.6		
1		R	Pass	8	**11.3**	1.0	8	**8.6**	0.6	2.29	.045
2–3	M	G	Pass	10	**11.4**	0.7	10	**9.9**	0.8		
2–3	M	R	Pass	8	**14.1**	1.8	7	**9.1**	1.2	2.30	.042
4–5	F	G	Pass	8	**13.3**	1.0	8	**12.4**	0.3		
5+	F	G	Pass	9	**12.7**	0.9	8	**12.2**	0.9		
5+	F	G	Sterpi	7	**18.0**	1.8	6	**17.5**	1.9		

Difference in the same direction in all 7 sets; $p < 0.05$, Sign Test.

why they go on to move away earlier than grazing animals, unless having risen somehow predisposes them to move.

The longer flight distances in resting females with kids, compared to those without, may reflect the vulnerability of the young, which were only a month old and had just emerged on the meadows from the cliff nursery areas. CEDERNA and LOVARI (unpublished) found similarly that alert distance was significantly greater in flocks containing a large proportion of kids.

Flight distances decreased in the course of the study, presumably as the animals habituated to the same person moving quietly among them in a predictable way. It is also possible that the observer was learning how to approach more effectively, but care was taken to maintain a uniform technique throughout the study. The failure of ear-tagged and other individuals approached several times to show any consistent decrease in flight distance may be due to the small number of approaches to each animal and the long gaps between some of the successive tests. McLAREN and GREEN (1985) similarly found no consistent effect of repeated approaches to musk oxen *Ovibos moschatus*.

Habituation effects can explain the differences in flight distance between areas, with the shortest in the area most visited by people (Pass) and the longest in the most remote area (Mt. Amaro), where there was also the possibility of some poaching (S. LOVARI, pers. comm.). In the main study areas, CEDERNA and LOVARI (unpublished) showed a decrease in mean flight distance from 25 m in 1977–78 to 19 m in 1981–82. This reduction has apparently continued, to the 11 m found in the present study, presumably as the animals have continued to habituate to the close proximity of people.

The results of this study are encouraging for the conservation of chamois; younger animals appear not to be more affected by disturbance than older ones, as had been feared, and flocks in close proximity to heavily visited areas appear to be habituating progressively to human presence. Recent improvements in visitor control in the Val di Rose, whereby in the busiest period (July and August) visitors are mainly confined to guided parties restricted to the marked trails by increased wardening, seem greatly to have reduced the kind of harassment of the animals described by CEDERNA and LOVARI (1985). Continued "benign" exposure to people should encourage further habituation of the animals and so reduce the effects of visitors on them.

Acknowledgements

I am indebted to Professor SANDRO LOVARI for his invaluable help and advice and to the Director of the Abruzzo National Park for permission to work there. The study was supported financially by Aberdeen University, The Carnegie Trust and The Royal Society.

Zusammenfassung

Reaktionen apenninischer Gemsen auf menschliche Störung

Diese Untersuchung befaßte sich mit der Wirkung menschlicher Störung auf das Verhalten verschiedener Altersgruppen von apenninischen Gemsen, *Rupicapra pyrenaica ornata*, in drei Regionen mit verschieden häufiger menschlicher Anwesenheit im oberen Val di Rose, Abruzzo Nationalpark, Italien, im Juli 1986.

Bei standardisierten Annäherungsversuchen wurde kein signifikanter Unterschied bei den Fluchtdistanzen zwischen Männchen und Weibchen oder zwischen grasenden und ruhenden Tieren gefunden, aber die Fluchtdistanzen von einjährigen und sub-adulten Gemsen waren statistisch bedeutend kürzer als die von jungen Adulten. Weibchen mit Jungen hatten statistisch größere Fluchtdistanzen als Weibchen ohne Junge, obwohl dieser Unterschied nur ruhende Tiere betraf. Die Fluchtdistanzen waren am kürzesten in der am häufigsten besuchten Region und am größten in der abgelegensten. Es gab Anzeichen dafür, daß wiederholte Begegnung mit Menschen zur Gewöhnung führte.

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Z. Säugetierkunde 53 (1988) 253–255

ISSN 0044-3468

WISSENSCHAFTLICHE KURZMITTEILUNG

First record of the Pygmy killer whale, *Feresa attenuata* Gray, 1875 from Peru, with a summary of distribution in the eastern Pacific

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Receipt of Ms. 10. 11. 1987

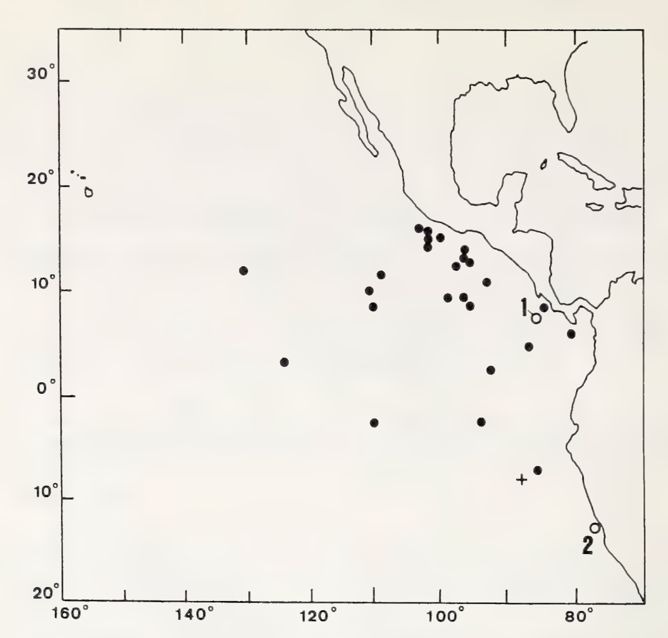
The distribution of the pygmy killer whale, *Feresa attenuata* Gray, 1875 was reviewed by Perrin and Hubbs (1969) and by Ross and Leatherwood (in press), and is assumed to be circumglobal in tropical and subtropical waters. The first record of this species from the eastern Pacific was a juvenile captured in May 1967 during commercial tuna fishing operations 300 to 400 nautical miles off Costa Rica (Perrin and Hubbs 1969). National Marine Fisheries (NMFS) observers aboard U.S.-registered tuna purse seiners operating in the eastern tropical Pacific reported 25 sightings of pygmy killer whales in the period 1971–1985 (as summarized in the Figure; Perrin, pers. comm.). *Feresa* is not seen in the northern part of the tuna grounds, towards the Gulf of California. Only three sightings are from south of the equator, where NMFS survey effort has been comparatively low: 25 animals at 02° 32′S, 94° 11′W on 17 January 1979; 9 at 07° 20′ S, 85° 13′ W on 6 December 1980, and 15 at 02° 27′ S, 109° 58′ W on 15 March 1981. In addition, during the IWC/IDCR research cruise in the eastern tropical Pacific in November and December 1982, one school of 8 animals without calves was seen at 08° 37′ S, 88° 04′ W (Donovan 1984).

Data are presented below on the first report of the pygmy killer whale from Peru, the most southerly record of this species in the eastern South Pacific.

On 30 November 1984 the mummified remains of a pygmy killer whale were discovered in one of the several dumps in the desert surrounding Pucusana, a small fishing town in central Peru (12° 30′ S, 76° 48′ W). At the same place, many tens of skeletons of several other small cetaceans were found, all victims of the Peruvian small cetacean fishery. In Pucusana most small cetaceans are caught in gill nets, with the remainder captured by a variety of other methods (Read et al. 1985; Van Waerebeek and Reyes 1986; Van Waerebeek et al. 1987). The majority of local fishing occurs well within 100 nautical miles of shore and mostly much closer.

The *Feresa attenuata* specimen we report consists of the head, the hyoids, six posterior lumbar vertebrae, the complete series of caudals (32), 23 chevron bones, both pelvic bones, the flippers, and the dorsal fin. The intact skull, covered by mummified skin, showed the rounded head typical of this species; all underlying soft tissue had disappeared. Sex and total length of the animal could not be determined. Initially the animal was thought to be physically immature considering the small size of the skull (339 mm condylobasal length) compared to the 352–405 mm range (X = 373 mm, n = 27) listed by Ross and Leatherwood (in press). However, fusion of the epiphyses of the caudal and lumbar vertebrae as well as in the flipper bones, the near closure of tooth pulp cavities, the flattening of the dorsal surface of the rostral portion of the premaxillae lying on the same

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Summary of known distribution of *Feresa attenuata* in the eastern Pacific: ● = sightings by NMFS observers between 1971–1985 (Perrin, pers. comm.); + = sighting during IWC/IDCR research cruise (Donovan 1984); 1 = specimen collected off Costa Rica (Perrin and Hubbs 1969); 2 = specimen from Pucusana, Peru (present paper). Central Pacific records (e.g. Hawaii) are not shown here

level as the maxillae (sensu Fraser 1960), and the general degree of fusion of the cranial sutures all indicate that the whale was at least approaching physical maturity.

Cranial measurements (in mm) according Schnell et al. (1982), and as a percentage of the condylobasal length (CBL) shown in parentheses, are: CBL, 339 (100); length of rostrum from base, 161 (47.5); length of rostrum from pterygoid, 203 (59.9); width of rostrum at base, 122 (36.0); width of rostrum at ¼ length, 98 (28.9); width of rostrum at ½ length, 86 (25.4); width of premaxillaries at ½ length, 57 (16.8); width of rostrum at ¾ length, 69 (20.4); preorbital width, 203 (59.9); postorbital width, 233 (65.8); skull width at zygomatic process, 224 (66.1); skull width at parietals, 164 (48.4); height of braincase from basisphenoid to summit of supraoccipital, excluding crest, 113 (33.3); internal length of braincase, including occipital condyles, 138 (40.7); maximum width of premaxillaries, 85 (25.1); greatest width external nares, 46 (13.6); length mesethmoid, 60 (17.7); greatest width of left temporal fossa, 63 (18.6); orbital length, 59 (17.4); length of left antorbital process, 44 (13,0); maximum separation of pterygoids, 1 (0.3); greatest width of internal nares, 58 (17.1); length of left tympanic cavity, 64 (18.9); length of right tympanic cavity, 63 (18.6); greatest distance between left and right pterygobasioccipital sutures, 59 (17.4); length left upper tooth row, 108 (31.9); number of teeth-upper left, 10; -upper right, 9; -lower left, 11; -lower right, 12; length of left lower tooth row, 120 (35.4); greatest height of left ramus, 72 (21.2); tooth width, 5.8; greatest length of left ramus, 269 (79.3).

Both left and right pterygoid sinuses were eroded in "basket like" lesions as associated with infections of the nematode, *Crassicauda* sp. The damage to the bone could be diagnosed as severe (Perrin and Powers 1980).

The specimen is provisionally kept by the authors at their cetacean study collection in Lima under no. KVW-032.

The discovery of a pygmy killer whale combined with several other recent findings of pelagic, warm-water adapted small cetaceans on the coasts of Peru and Chile (Van

WAEREBEEK and REYES 1986; GUERRA et al. in press), suggest that the Humboldt Current is more a heterogenous and highly variable water body than a continuous and impenetrable cold water barrier.

Acknowledgements

W. F. PERRIN, G. J. B. ROSS and S. LEATHERWOOD are thanked for generously supplying unpublished data. The same persons and P. J. H. VAN BREE made several very useful comments on a previous draft of this note. Funding came from a 1984 research grant to K. VAN WAEREBEEK by the "Leopold III-Fonds voor Natuuronderzoek en Natuurbehoud" (Brussels), through A. CAPART and J.-P. GOSSE of the "Institut Royal de Sciences Naturelles de Belgique". Logistical support was provided by B. A. LUSCOMBE of ECCO and by J. G. MEAD and C. W. POTTER of the Smithsonian Institution, Washington, D.C.

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BUCHBESPRECHUNG

Grzimek, B. (Hrsg.): **Grzimeks Enzyklopädie Säugetiere – Band 4.** München: Kindler-Verlag 1987. 648 S., zahlreiche Abb., Lexikon-Großformat. Leinenausgabe: Subskriptionspreis DM 128,–, später DM 148,–, ISBN 3-463-42004-X; Luxusausgabe (Halbleder): Subskriptionspreis DM 168,–, später DM 198,– ISBN 3-463-42104-6

Mit „Grzimeks Enzyklopädie Säugetiere" ist ein voluminöses, fünfbändiges Werk konzipiert, das in Erweiterung der vier 1970 erschienen Säugetierbände aus „Grzimeks Tierleben" andere Akzente setzt. Neben einer verständlichen Vermittlung allgemeiner biologischer Sachverhalte über Säugetierarten sind vor allem neuere Erkenntnisse aus den Gebieten Stammesgeschichte, Ökologie und Ethologie Anliegen der Abhandlungen sowie Häufigkeit und Bedrohung der Arten und ihre Beziehungen zum Menschen. Aus redaktionellen Gründen liegt als erstes nun der 4. Band vor. Er behandelt in Fortsetzung der Carnivora die Pantherkatzen und Verwandte, die Canidae und die Pinnipedia, des weiteren die Ordnungen Lagomorpha, Cetacea, Tubulidentata, Proboscidea, Hyracoidea, Sirenia, Perissodactyla. Die Beschreibungen der Ordnungen erfolgen nach einheitlicher Gliederung in Einleitung, Stammesgeschichte und Abhandlung über die allgemeine oder besondere Biologie der Arten. Den Kapiteln vorangestellt sind sog. Basisinformationen, die kurzgefaßt einen Überblick über gruppenspezifische Besonderheiten darlegen. Zusätzlich ermöglichen tabellarisch gegenübergestellte Angaben über Körpermaße, Merkmale, Fortpflanzung, Lebenslauf, Nahrung, Feinde, Lebensweise und Lebensraum schnelle und detaillierte Information über einzelne Arten. Im Text wird auf ältere und neuere Erkenntnisse biologischer Besonderheiten eingegangen, ferner auf die Bedeutung vieler Arten in der Mythologie der Völker, ihre Nutzung durch den Menschen in Vergangenheit und Gegenwart, rezente Bestandsentwicklungen, Maßnahmen bei Bestandsbedrohungen und vieles andere mehr. Verbreitungsskizzen der meisten Arten und eine besonders attraktive und beeindruckende Ausstattung mit Situationsaufnahmen aus freier Wildbahn unterstützen die Beschreibungen. Fremdwörter und Fachausdrücke wurden vermieden oder verständlich, wenn auch nicht immer einheitlich erklärt.

Die Bearbeitung der Arten und systematischen Gruppen dieses Bandes ist auf 23 Autoren aufgeteilt. Die Abschnitte fallen dementsprechend unterschiedlich aus sowohl in der Form der Darstellung als auch in der inhaltlichen Gewichtung. Während in einigen Kapiteln eine stärker erzählende, mit eigenen Erlebnissen angereicherte Darstellungsform überwiegt, wird in anderen auf knapp gefaßte und sachliche Vermittlung von Information Wert gelegt. Die Mehrzahl der taxonomischen Gruppen wurde von wenigen Autoren bearbeitet, so daß diese Unterschiede kaum als störend empfunden werden. Die Kapitel wirken in sich geschlossen und machen einen abgerundeten Gesamteindruck. In der Regel sind alle bekannten Arten taxonomischer Gruppen erwähnt und unserem Wissensstand entsprechend mehr oder weniger ausführlich gekennzeichnet. Bei den Lagomorpha stehen allerdings die Arten *Lepus europaeus* und *Oryctolagus cuniculus* übergewichtig im Zentrum. Wenig Information erhält man in dieser Ordnung über andere Arten der Leporidae, und auch die Ochotonidae sind vergleichsweise kurz dargestellt. Auf besonders breitem Raum von über 100 S. und mit einer besonders starken „Zersplitterung" der Bearbeitung unter mehreren Autoren, die in abwechselnder Reihenfolge zu Wort kommen, sind die Canidae abgehandelt. In diesem Abschnitt können an mehreren Stellen Wiederholungen, inhaltliche Widersprüche und als wissenschaftlich belegt ausgewiesene, spekulative Ansichten zu Verunsicherungen führen oder als störend empfunden werden. Ferner zeigt der Band in bestimmter anderer Hinsicht eine etwas unausgewogene Konzeption oder Bearbeitung, denn ein Leser, der an Haus- und Nutztieren interessiert ist, wird vergleichsweise detailliert über Haushunde informiert, in deutlich geringerem Maße über Hausesel und Hauspferde, so gut wie überhaupt nicht jedoch über Hauskaninchen. Unerwähnt bleibt auch die Bildung zahlreicher Farbschläge von Farmfüchsen. Auf die Nutzung von Rot- und Eisfuchs als Pelztiere wird nur kurz in unbewiesener und emotionaler Weise, der aktuellen Diskussion um Pelztierhaltung kaum förderlich, eingegangen.

Im Hinblick auf den Umfang des Bandes fallen die angeführten Mängel jedoch kaum ins Gewicht, denn insgesamt liegt eine schöne und informative Dokumentation auf modernem Wissensstand vor, die ein Verständnis für die besondere Biologie der behandelten Arten fördert. Das Anliegen des Verlages, ein Tierlesebuch, ein Tierbilderalbum und ein Tierlexikon in einem Werk zu erstellen, kann grundsätzlich als gelungen bewertet werden. Es wird sicherlich von interessierten Laien und Fachleuten mit Gewinn genutzt werden.

D. Kruska, Kiel



Erscheinungsweise und Bezugspreis 1988: 6 Hefte bilden einen Band. Jahresabonnement Inland: 308,– DM zuzüglich 13,80 DM Versandkosten, Gesamtpreis 321,80 DM einschließlich 7 % Mehrwertsteuer. Jahresabonnement Ausland: 308,– DM zuzüglich 18,– DM Versandkosten. Das Abonnement wird zum Jahresanfang berechnet und zur Zahlung fällig. Es verlängert sich stillschweigend, wenn nicht spätestens am 15. November eine Abbestellung im Verlag vorliegt. Die Zeitschrift kann bei jeder Buchhandlung oder bei der Verlagsbuchhandlung Paul Parey, Spitalerstraße 12, D-2000 Hamburg 1, bestellt werden. Die Mitglieder der „Deutschen Gesellschaft für Säugetierkunde“ erhalten die Zeitschrift unberechnet im Rahmen des Mitgliedsbeitrages.

Z. Säugetierkunde 53 (1988) 4, 193–256

Vol. 53 (5), 257–320, Oktober 1988 ISSN 0044-3468 C 21274 F

ZEITSCHRIFT FÜR SÄUGETIERKUNDE

INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Organ der Deutschen Gesellschaft für Säugetierkunde



Verlag Paul Parey Hamburg und Berlin

This journal is covered by Biosciences Information Service of Biological Abstracts, and by Current Contents (Series Agriculture, Biology, and Environmental Sciences) of Institute for Scientific Information

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Zusätzlich erscheint einmal im Jahr ein Heft mit den Abstracts der Vorträge, die auf der jeweiligen Hauptversammlung der Deutschen Gesellschaft für Säugetierkunde gehalten werden. Sie werden als Supplement dem betreffenden Jahrgang der Zeitschrift zugeordnet. Verantwortlich für ihren Inhalt sind ausschließlich die Autoren der Abstracts.

Manuskripte: Manuskriptsendungen sind zu richten an die Schriftleitung, z. Hd. Prof. Dr. Dieter Kruska, Institut für Haustierkunde, Biologie-Zentrum, Neue Universität, Olshausenstr. 40–60, D-2300 Kiel. Für die Publikation vorgesehene Manuskripte sollen gemäß den „Redaktionellen Richtlinien" abgefaßt werden. In ihnen finden sich weitere Hinweise zur Annahme von Manuskripten, Bedingungen für die Veröffentlichung und die Drucklegung, ferner Richtlinien für die Abfassung eines Abstracts und eine Korrekturzeichentabelle. Die Richtlinien sind auf Anfrage bei der Schriftleitung und dem Verlag erhältlich.

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Fortsetzung 3. Umschlagseite

 Verlag: Paul Parey, Hamburg und Berlin. Anschriften: Spitalerstr. 12, D-2000 Hamburg 1; Lindenstr. 44–47, D-1000 Berlin 61. – Printed in Germany by Westholsteinische Verlagsdruckerei Boyens & Co., D-2240 Heide/Holst.

Z. Säugetierkunde 53 (1988) 257–266

ISSN 0044-3468

Ergebnisse automatischer Aktivitätsaufzeichnungen an Wochenstubenkolonien der Bechsteinfledermaus (*Myotis bechsteini*)

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Eingang des Ms. 9. 6. 1987

Abstract

Results of automatically monitoring Bechstein bats' activities

Studied activities of *Myotis bechsteini* at their roosting sites. Using a newly developed data-acquisition system, the activities of Bechstein bats *(Myotis bechsteini)* were monitored during 27 observation nights in northern Bavaria. The following results were obtained: 31–34 min after sunset, one half of a bat colony left for foraging. Bats started to leave the nest boxes at a luminance level of about 14 lux, and 50 % had left by 0.4 lux. The Bechstein bats' outburst pattern was characterized by departure in groups of several individuals. Both the colony size and environmental factors such as low ambient temperatures influenced the bats' outburst behavior. Bechstein bats' activities in front of their roosting nest boxes diminished during the night as the young got older. Bechstein bats returned to a roost 110 min before sunrise. Sixty to forty min before sunrise, the activities peaked in front of the roost; and at 20 min before sunrise, all bats had returned.

Einleitung

Als versteckt lebende Baumfledermaus ist die Bechsteinfledermaus *(Myotis bechsteini* Leisler in Kuhl, 1818) einer Beobachtung bei abendlichem Ausflug und nächtlicher Aktivität schwer zugänglich. Im Bereich des Forstamtes Ebrach im nördlichen Steigerwald (Nordbayern) nimmt *Myotis bechsteini* Nistkästen als Quartier an. Charakterisiert durch häufigen Quartierwechsel (Wolz 1986) besiedeln die Fledermäuse ab Ende Juli eine Reihe von Vogelnistkästen im Forstrevier, bis sie Ende September wieder verschwinden und sich entweder in unzugängliche Baumquartiere zurückziehen oder das Gebiet verlassen. Mit Hilfe von Infrarotlichtschranken-Ereignisspeichern – entwickelt am II. Zoologischen Institut der Universität Erlangen – konnten abendlicher Ausflug, nächtliche Aktivität am Nistkasten und morgendliche Rückkehr aufgezeichnet werden. Dieses automatische Datenerfassungssystem ermöglicht mit vertretbarem Arbeitsaufwand Registrierungen der Fledermausaktivität über längere Zeit.

Material und Methode

Drei verschiedene Wochenstubenkolonien der Bechsteinfledermaus, die sich – an den Ringnummern erkenntlich – nicht mischen, besiedeln den Winkelhofer Forst im nördlichen Steigerwald, einen Laubmischwald mit abwechslungsreicher Waldstruktur. Einzelne Gruppen aus diesen Kolonien – in der Regel adulte Weibchen mit Jungtieren – suchen 30 von insgesamt 575 vorhandenen Nistkästen bevorzugt auf. An 9 dieser Nistkästen konnten in den Jahren 1984 bis 1986 mit Hilfe einer Infrarot-Lichtschranke 27 Ausflugsbeobachtungen durchgeführt werden, wobei insgesamt 636 Registrierungen beim abendlichen Ausflug aufgezeichnet wurden. Der Schwerpunkt lag auf der Überwachung des Nistkastens, der von allen im Forstamt Ebrach angebrachten Nisthilfen von *Myotis bechsteini* am häufigsten als Quartier genutzt wurde (15 Ausflugsbeobachtungen mit insgesamt 403 registrierten Individuen). In 10 Fällen wurde zusätzlich zur nächtlichen Aktivität auch die morgendliche Rückkehr

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von Fledermäusen erfaßt. Die Koloniegröße war starken Schwankungen unterworfen und betrug mindestens 6, maximal 51 Individuen; die Beobachtungen beschränkten sich jeweils auf die Monate August und September, außerhalb dieses Zeitraumes waren Bechsteinfledermäuse nur gelegentlich in Nistkästen anzutreffen. Alle Zeitangaben erfolgen in mitteleuropäischer Sommerzeit, MESZ.

Der Lichtschranken-Ereignisspeicher

Um die Probleme mechanischer Schreiber (begrenzte Zeitauflösung, hoher Papierverbrauch) zu umgehen, wurde für die vorliegenden Untersuchungen am II. Zoologischen Institut der Universität Erlangen-Nürnberg ein Infrarotlichtschranken-Ereignisspeicher (IR-LES) entwickelt, der aus den Modulen: 1. Lichtschranken-Rahmen mit IR-Sende- und Empfangselektronik, 2. Ereignisklassifizierungs- und Speichereinheit mit Echtzeituhr sowie 3. Datendisplay und Ausgabeeinheit besteht. Aus Stabilitätsgründen wurden Metallrahmen zur Halterung der Sende- und Empfangsdioden entworfen, welche an die Abmessungen der im Forstamt Ebrach verwendeten Nistkästen angepaßt sind (Bayerischer Spitzgiebelkasten der Fa. Grund, Fluglochöffnung oval, 3 cm × 5 cm). Diese Konstruktion gewährleistet, daß die Schranke rasch am Nistkasten angebracht und justiert werden kann, ohne daß die Fledermäuse durch Erschütterungen gestört werden. Abb. 1 zeigt die Lage der beiden IR-Strahlen relativ zur Fluglochöffnung.

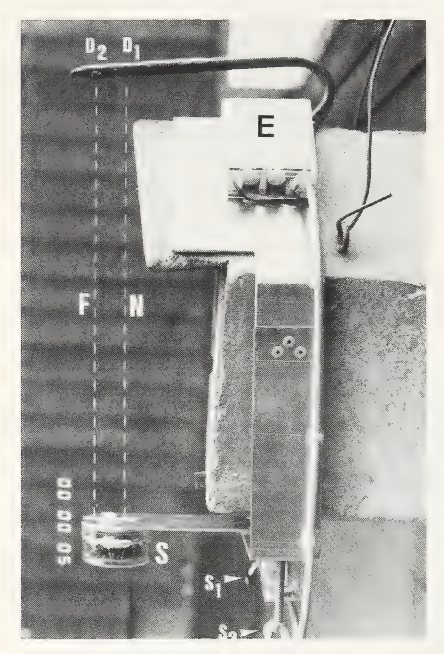


Abb. 1. Lichtschranken-Rahmen am Nistkasten. Sender- und Empfängerelektronik („S", „E") sind regensicher untergebracht. Die Lage beider IR-Strahlen („N", „F") zwischen den Empfangsdioden D_1, D_2 und den Sendedioden wird durch die unterbrochenen Linien markiert. Mit den Stellschrauben S_1 und S_2 kann der Lichtschranken-Rahmen schnell und geräuschlos am Nistkasten befestigt werden. Der Bereich zwischen „N"-Strahl und Nistkastenfront stellt die Zone dar, in der sich die Fledermäuse hinter den IR-Strahlen bewegen können, ohne registriert zu werden

Die Richtungserkennung eines Durchfluges erfolgt durch Vergleich der beiden Empfängersignale, ein ‚Ereignis' beginnt mit der Unterbrechung des ‚N'-Strahls (s. Abb. 1). Aus dem Zustand des nistkastenfernen ‚F'-Strahls zu den Zeitpunkten ‚N-Strahl-Unterbrechung' und ‚N-Strahl-Freigabe' ergibt sich die gewünschte Ereignisunterscheidung in ‚Einflug' und ‚Ausflug'.

Das Verhalten der Fledermäuse beim Ausflug ins Jagdgebiet – schnelles Abspringen vom Flugloch – erlaubt am Abend die exakte Zählung der Individuen einer Wochenstubenkolonie. Der Einflug ins Quartier während der Nacht und am Morgen erfolgt jedoch erst nach einer Reihe von An- und Abflügen am Nistkasten. Ein- und Ausflugsregistrierungen heben sich bei den ‚Probeanflügen' nicht immer auf. Ursache hierfür ist folgendes beobachtete Verhalten: Die Fledermäuse fliegen das Flugloch frontal an, schlüpfen jedoch nicht ein, sondern lassen sich nach unten fallen und fliegen nach hinten ab, ohne die IR-Strahlen noch einmal in Ausflugsrichtung zu durchkreuzen. Diese Strahlenanordnung erlaubt somit die präzise Ausflugszählung sowie die Überwachung der Flugaktivitäten vor dem Nistkasten im Verlauf einer Nacht.

Helligkeitsmessungen

Zur Helligkeitsmessung während der Aktivitätsaufzeichnungen wurden folgende Geräte verwendet: 1. Gossen, Mod. Mavolux digital (Beleuchtungsstärkemeßgerät, Messung in lx), 2. Digital-Luxmeter, IC-Sensor Siemens TFA 1001 (Beleuchtungsstärke-Meßgerät), 3. Li-Cor, Mod. LI-185B, Sensor LI-200SB (Bestrahlungsstärke-Meßgerät, Messung in W/m^2). Die Bestrahlungsstärke spiegelt die gesamte einstrahlende Leistung pro Fläche wider, berücksichtigt also auch alle nicht sichtbaren Anteile im UV- und IR-Bereich. Die Beleuchtungsstärke gibt nur den sichtbaren Anteil der einfallenden Strahlung an und bewertet das Spektrum mit der international festgelegten Gewichtungskurve $V(\lambda)$, welche die spektrale Empfindlichkeit des menschlichen Auges – und nicht des Fledermausauges – berücksichtigt. Einige Vergleichswerte sollen zur besseren Vorstellung der in der vorliegenden Untersuchung angegebenen Helligkeiten dienen: Sonnenlicht im Sommer 100 klx, im Winter 10 klx, bedeckter Himmel im Sommer 5 klx bis 20 klx, Nacht bei Vollmond 200 mlx, mondlose, klare Nacht 0,3 mlx (Kuchling 1982).

Ergebnisse

Zeitpunkt und Dauer des abendlichen Ausflugs

Abb. 2 zeigt alle Ausflugsregistrierungen am beliebtesten Nistkasten der größten *Myotis-bechsteini*-Kolonie. Dargestellt ist die Summe der Ausflüge in der i-ten min nach Sonnenuntergang (SU), summiert über N Beobachtungsnächte. Die dunklen Säulen geben die Ausflugsbeobachtungen von 10 Abenden mit vergleichbaren Witterungsverhältnissen und bei mittleren Koloniegrößen wieder. Man erkennt, daß die ersten ausfliegenden Fledermäuse ab der 13. min nach Sonnenuntergang registriert wurden, die Anzahl der das Quartier verlassenden Tiere schnell zunahm und sich dabei relativ hohe Zahlen ausfliegen-

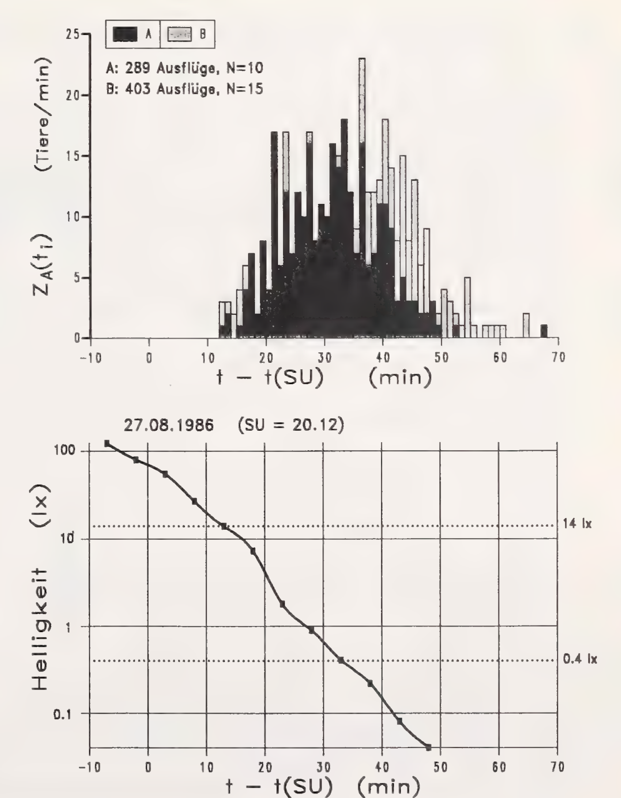


Abb. 2. Abendlicher Ausflug am beliebtesten Nistkasten der größten *Myotis-bechsteini*-Kolonie. Helle Säulen: Zusammenfassung der Ausflugsregistrierungen an allen N Beobachtungsabenden (N = 15). Helle Säulen erreichen auf Grund der Summendarstellung mindestens die Höhe dunkler Säulen, da gilt:

$$Z_A(t_i) = \sum_{k=1}^{N} S_k(t_i) = N * R_N(t_i).$$

$Z_A(t_i)$: Summe der Ausflüge in der i-ten min nach Sonnenuntergang in N Nächten; $S_k(t_i)$: Ausflüge in der i-ten min nach SU in der k-ten Nacht; $R_N(t_i)$: Mittelwert der Ausflüge in der i-ten min nach SU, gemittelt über N Nächte; dunkle Säulen: Summendarstellung von 10 Ausflugsbeobachtungen an Kolonien mittlerer Größe unter gleichen Witterungsbedingungen (N = 10, Teilmenge von (B); obere Kurve: Abnahme der Helligkeit vor dem Nistkasten am 27. 8. 1986 bei bewölktem Himmel

der Individuen mit jeweils im Vergleich dazu niedrigen Werten abwechselten. Hier wird trotz der Summierung von 10 Beobachtungsabenden das pulkweise Ausfliegen der Bechsteinfledermäuse noch deutlich. 50 % aller Fledermäuse sind im Mittel 31.5 min nach Sonnenuntergang ausgeflogen. Mit hellen Säulen zeigt Abb. 2 die Gesamtheit aller Ausflugsbeobachtungen an diesem Nistkasten einschließlich der Ausflüge, die vom Normalverhalten deutlich abwichen (z.B. sehr große oder sehr kleine Fledermausgruppen). Im Vergleich zu der mit dunklen Säulen dargestellten Teilmenge (Beobachtungen bei mittlerer Koloniegröße) verschiebt sich das zeitliche Mittel geringfügig: 34 min nach Sonnenuntergang haben bei Berücksichtigung aller Ausflugsregistrierungen (insgesamt 403) 50 % der Fledermäuse das Quartier verlassen.

An 7 von 27 Beobachtungsabenden verließen die ersten Individuen schon vor der 20. min nach SU (frühestens in der 12. min nach SU) das Quartier. An 15 von 27 Abenden begann der Ausflug der Bechsteinfledermäuse zwischen der 20. und 30. min nach SU. Ausflugsbeginn eine halbe Stunde nach Sonnenuntergang oder später war dagegen selten und bis auf eine Ausnahme auf kleine Fledermausgruppen mit weniger als 10 Individuen beschränkt.

Mit der Individuenzahl der Fledermausgruppen im Nistkasten stieg sowohl die Dauer des Ausfluges wie auch die Ausflugsrate (d.h. die Zahl der ausfliegenden Tiere pro Zeiteinheit). Im Falle kleiner Gruppen (ca. 5 Individuen) verließen im Mittel 0,5 Tiere/min das Quartier, die mittlere Ausflugsrate großer Gruppen (ca. 40 Tiere) betrug hingegen 2 Tiere/min. Das Abfliegen der Fledermäuse verlief nicht gleichmäßig; bei mittleren oder großen Gruppen bildeten sich häufig Pulks aus 3 bis 5 Fledermäusen. Diese Tiere flogen in zeitlichen Abständen von wenigen Sekunden aus.

Bestimmende Faktoren des Ausflugsbeginns

Es ist bekannt, daß die abendlichen Lichtverhältnisse und das schnelle Absinken der Helligkeit während der Dämmerung eine Schlüsselfunktion bei der Bestimmung des Ausflugsbeginns einer Fledermauskolonie einnehmen (Engländer und Laufens 1968; DeCoursey und DeCoursey 1964; Swift 1980; Voûte et al. 1974; u.a.).

Abb. 2 zeigt die Abnahme der Helligkeit (obere Kurve) am 27. 8. 1986 (bewölkter Himmel) in der Nähe des Nistkastens, an dem die der Graphik zu Grunde liegenden Ausflugsbeobachtungen durchgeführt wurden. Es zeigt sich an der Summendarstellung, daß im Mittel 50 % der Fledermäuse den Nistkasten zum Jagdflug verlassen hatten, bevor 33 min nach Sonnenuntergang die Helligkeitswerte unter 0,4 lx absanken. Die früh ausfliegenden Fledermäuse (ab der 13. min nach SU, 14 lx am 27. 8. 1986) bewegten sich in allen drei Beobachtungsjahren noch im hellen Dämmerlicht und waren mit bloßem Auge gut erkennbar, bis sie beim Abflug ins Jagdgebiet hinter Laubwerk verschwanden. Im Jahr 1986 wurden Helligkeitsmessungen sowohl bei vollständig bedecktem wie auch bei klarem Himmel – mit durchziehenden Wolkenfeldern – durchgeführt. Während der frühen Dämmerung war der Einfluß der Bewölkung auf die gemessenen Helligkeitswerte ausgeprägt beobachtbar. Der Helligkeitsbereich, bei dem Bechsteinfledermäuse ausflogen, ist jedoch zumindest für einzelne Individuen sehr groß und umfaßt nach Abb. 2 alle Werte unter 15 lx. Helligkeitsschwankungen zur Ausflugszeit durch aufziehende Wolkenfelder oder beginnenden leichten Regen beeinflußten das Verhalten der Fledermäuse nicht signifikant.

Im Gegensatz zu den Beobachtungen, die Laufens (1972) an einzeln lebenden Männchen der Bechsteinfledermaus machte, verhinderten starke Regenschauer zur normalen Ausflugszeit – am 26. 8. 1986 und am 28. 8. 1986 – den Aufbruch einer Wochenstubenkolonie nicht. Sowohl der Zeitpunkt des Ausflugsbeginns (13. bzw. 28. min nach SU) wie auch die Dauer des Ausflugs (33 Indiv. in 31 min bzw. 34 Indiv. in 37 min) unterschieden sich nicht signifikant von Beobachtungen bei schönem Wetter. Bemerkenswerterweise

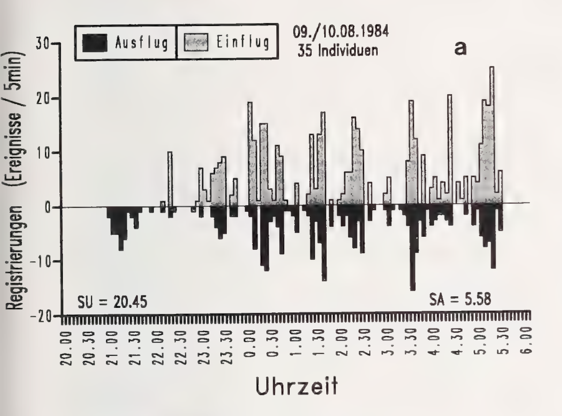
wies das Ausflugsgeschehen am 26. August allerdings die größte je registrierte Zahl langer Pausen auf (7 Pausen über 3 min).

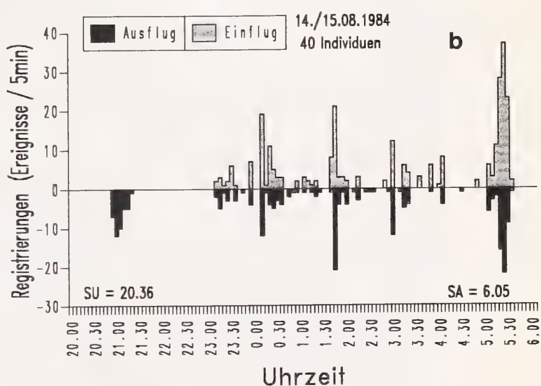
Deutliche Auswirkungen auf das Verhalten der Fledermäuse hatten hingegen niedrige Außentemperaturen, die den Ausflug um bis zu 20 min verzögerten bzw. ganz verhinderten. Die Abendtemperaturen – gemessen um 19 Uhr – nahmen vom 26. 8. 1986 (18 °C) bis zum 29. 8. 1986 (10 °C) deutlich ab. Drei Fledermäuse aus einer Gruppe von 7 Individuen flogen am 29. 8. stark verspätet aus (48.–54. min), die restlichen Tiere blieben während der gesamten Nacht im Quartier. Dieses Verhalten wurde bei vergleichbaren Temperaturverhältnissen auch in anderen Jahren beobachtet; teilweise flogen die Fledermäuse auch an zwei aufeinanderfolgenden Nächten nicht zum Jagdflug aus.

Ebenfalls Einfluß auf den Ausflugsbeginn scheint neben der Helligkeit und den Wetterbedingungen die Koloniegröße zu haben. Kleine Fledermausgruppen neigten zu spätem Ausflug ab 30 min nach SU. Auch zeigte die größte beobachtete Kolonie von *Myotis bechsteini* (51 Indiv.) ungewöhnliches Verhalten mit Ausflugsbeginn in der 36. min nach SU und sehr raschem Ausflug in 12 min. Es konnten jedoch keine statistisch signifikanten Daten ermittelt werden, da derart große Gruppen zu selten zu finden waren.

Aufzeichnungen zwischen abendlichem Ausflug und morgendlicher Rückkehr

Abb. 3 (a–c) zeigt das Verhalten einer Wochenstubenkolonie in drei Nächten des Jahres 1984. Der Nistkasten wurde im August 1984 15 Tage lang von den Fledermäusen ununterbrochen als Quartier benutzt. So war es möglich, Ausflug und Rückkehr der Bechsteinfledermäuse mehrmals hintereinander zu dokumentieren. Es zeigte sich, daß die





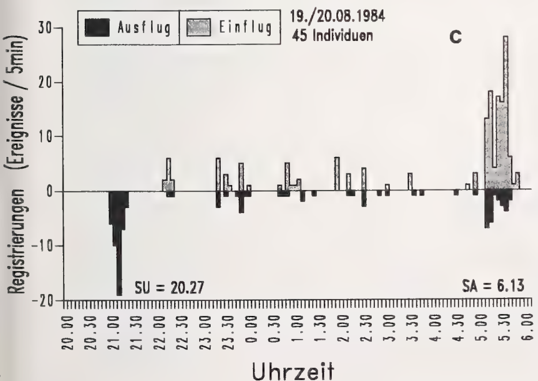


Abb. 3. Nächtliche Aktivität einer Kolonie von *Myotis bechsteini* im August 1984. a: In der Nacht vom 9. auf den 10. August 1984 herrscht vor dem Nistkasten während der ganzen Nacht heftige Aktivität durch an- und abfliegende Fledermäuse; b: In der Nacht vom 14. auf den 15. August 1984 zeichneten sich drei Aktivitätsmaxima ab; c: Zwischen dem Ausflug am 19. August 1984 und dem Einflug am 20. August 1984 wurden trotz großer Individuenzahl der Kolonie (45 Tiere) nur wenige Ereignisse während der Nacht registriert

nächtliche Aktivität am Nistkasten vom 9./10. August bis zum 19./20. August deutlich abnahm. Waren es in der ersten Beobachtungsnacht bei 35 Individuen noch 588 Ereignisse, verringerte sich diese Zahl in der Nacht vom 19. auf den 20. August bei einer Koloniegröße von 45 Individuen abends bzw. 37 Individuen morgens auf 83 Ereignisse. Vom 9. auf den 10. 8. 84 herrschte während der gesamten Nacht starke Aktivität vor dem Nistkasten, vom 14. auf den 15. 8. 84 waren noch drei Aktivitätsmaxima erkennbar, in der letzten Beobachtungsnacht registrierte der LES bis zum Einflug ab 5 Uhr nur vereinzelt Ereignisse. Am 24. 8. 1984 kehrten die Fledermäuse am Morgen nicht mehr in ihr Quartier zurück, einige Individuen flogen den Nistkasten ab 4 Uhr jedoch mehrmals an, die letzte Fledermaus wurde dabei 30 min vor Sonnenaufgang registriert. In zehn Nächten wurden Beobachtungen an quartierwechselnden Kolonien aufgezeichnet, die Zahl der Registrierungen am bisherigen Tagesquartier blieb in der Regel kleiner als 10 – nur in einer Nacht kehrte keine Fledermaus zurück. Die meisten Tiere suchten den verlassenen Nistkasten erst zur normalen morgendlichen Einflugszeit auf (in 6 von 9 Fällen), flogen aber wieder ab. Die späteste Fledermaus erschien dabei – offensichtlich auf der Suche nach ihrer Kolonie – 5 min vor Sonnenaufgang.

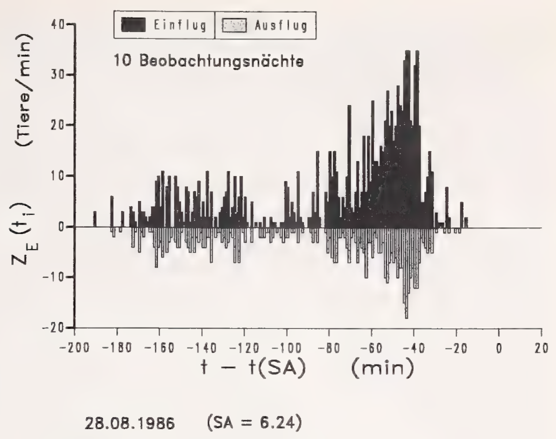
Morgendlicher Einflug der Tiere

In 10 Nächten (Aug. 84, Aug./Sept. 85, Aug. 86) gelang es, auch das morgendliche Rückkehrverhalten der Bechsteinfledermäuse zu dokumentieren. Abb. 4 zeigt die Zusammenfassung von 10 Einflugsbeobachtungen und die gemessenen Helligkeitswerte kurz vor Sonnenaufgang (SA). 110 min vor SA setzte der Einflug der Fledermäuse ein; 60–40 min vor SA herrschte die größte Aktivität vor dem Nistkasten, ab 30 min vor SA fanden nur noch einzelne Einflüge statt. Die Aufzeichnungen der zwischen drei und zwei Stunden vor Sonnenaufgang zurückkehrenden Fledermäuse stammen von Beobachtungen in der jeweils ersten Augusthälfte und sind vermutlich auf Aktivitäten von Jungtieren zurückzuführen. Je später die Aufzeichnungen im August erfolgten, desto deutlicher zeichnete sich der morgendliche Einflug zwischen der 80. und 30. min vor SA ab (s. Abb. 3). Die Helligkeitswerte während des Einflugs am 28. 8. 86 zeigt die obere Kurve in Abb. 4.

In mehreren Fällen wurde die Rückkehr der Fledermäuse (mit Nachtsichtgerät bzw. bei ausreichender Helligkeit mit bloßem Auge) beobachtet und gleichzeitig die Ereignisse mit dem LES dokumentiert. Dies geschah z.B. am 29. 8. 84, als eine kleine Gruppe von 10 Bechsteinfledermäusen in ihr vorheriges Tagesquartier zurückkehrte. Um 5 Uhr – bei noch völliger Dunkelheit – umflogen bereits einzelne Fledermäuse in einer Höhe von 2 bis 4 m das Quartier, verschwanden häufig minutenlang, um mit zunehmender Helligkeit den Nistkasten immer näher zu umrunden. Dann begannen sie, das Flugloch seitlich und von vorn anzufliegen. Einzelne Individuen klammerten sich am Nistkasten vor dem Flugloch fest, ließen sich fallen und flogen wieder ab. Der LES zeichnete ab 5.15 Uhr die ersten Ereignisse auf, der Einflug von 10 Fledermäusen ergab insgesamt 32 Registrierungen, der letzte Einflug erfolgte um 6.07 Uhr (Sonnenaufgang am 29. 8. 1984: 6.26 Uhr). Während der Endphase des Einflugs ab 5.45 Uhr wurde als Maximum auf 13 Anflüge an das Flugloch nur 1 Einflug beobachtet.

Diskussion

In der bisherigen Literatur zum Themenkreis ‚Ausflugszeit', ‚Ausflugsverhalten' bzw. ‚Aktivitätsperiodik der Fledermäuse' finden sich nur vereinzelt Hinweise auf die Bechsteinfledermaus *(Myotis bechsteini)* (Kolb 1959; Laufens 1972; Laufens 1973b). Es handelt sich dabei um Beobachtungen an Einzeltieren und nicht wie in der vorliegenden Untersuchung an Wochenstubenkolonien. Die Meinung, daß Bechsteinfledermäuse erst



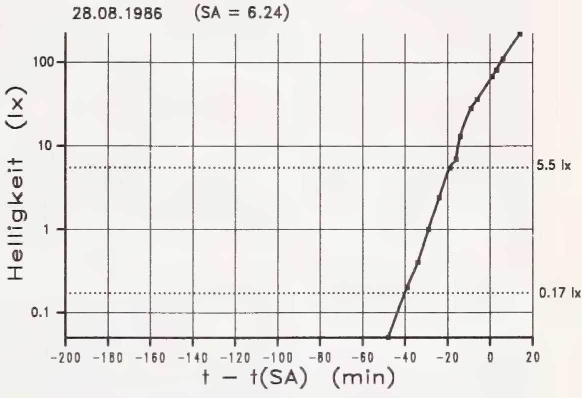


Abb. 4. Zusammenfassung von 10 morgendlichen Einflugsbeobachtungen am beliebtesten Nistkasten der größten *Myotis-bechsteini*-Kolonie. 60 bis 40 min vor Sonnenaufgang herrscht die größte Aktivität vor dem Nistkasten. Die Registrierungen zwischen 3 und 2 h vor Sonnenaufgang sind auf Rückflüge von Jungtieren während der ersten Augusthälfte zurückzuführen. $Z_E(t_i)$: Summe der Einflugsregistrierungen in der i-ten min vor Sonnenaufgang in 10 Nächten (zur Definition von $Z_E(t_i)$ vgl. Abb. 4, N = 10). Negative Werte: Ausflugsregistrierungen. Die obere Kurve zeigt die Zunahme der Helligkeit vor dem Nistkasten am 28. 8. 1986

nach Einbruch der Dunkelheit ausfliegen (Taake 1985), wurde durch das Verhalten von *Myotis bechsteini* im Steigerwald nicht bestätigt.

Der abendliche Ausflug erstreckte sich – abhängig von der Koloniegröße – teilweise über den gesamten Bereich der Dämmerung, die ersten ausfliegenden Individuen waren bei hohen Helligkeitswerten mit bloßem Auge gut erkennbar, während die letzten Fledermäuse in der Dunkelheit nur mit Hilfe automatischer Registrierung zu erfassen waren. Um die Ausflugszeit der Bechsteinfledermäuse mit der anderer Arten zu vergleichen, sind Angaben zur Ausflugszeit in Minuten nach Sonnenuntergang nicht geeignet, wenn nicht gleichzeitig Helligkeitsmessungen durchgeführt werden. So geben viele Autoren Zeiten zwischen 20 und 35 min nach Sonnenuntergang für die ersten ausfliegenden Tiere an: Zwergfledermaus, nördliches Schottland, 35 min: Swift (1980); Mausohr, FRG, 30 min: DeCoursey und DeCoursey (1964); Abendsegler in Dänemark, 20–30 min: v. Heerdt und Sluiter (1965); Teichfledermaus, >30 min, Niederlande: Voûte et al. (1974). Erst Helligkeitsmessungen machen die Unterschiede zwischen den Fledermausarten deutlich: Zwergfledermäuse fliegen bei Werten zwischen 15–35 lx aus (Swift 1980), Mausohren bei 20–100 mlx (DeCoursey und DeCoursey 1964), Teichfledermäuse zumeist bei Werten unter 350 $\mu W/m^2$ (Voûte et al. 1974). Die niedrigsten Helligkeitswerte für ausfliegende Tiere wurden für *Myotis nattereri* ermittelt, die nach Engländer und Laufens (1968) Ende August und im September erst 10–30 min nach Absinken der Helligkeit auf 1 mlx ihre Quartiere verlassen. *Myotis bechsteini* fliegt nach den Ergebnissen der vorliegenden Untersuchung in der Regel bei Helligkeitswerten unter 14 lx aus, 50 % der Individuen verlassen das Quartier nach Absinken der Helligkeit unter 0,4 lx. Die Ausflugswerte der Bechsteinfledermäuse sind daher am ehesten mit denen des Mausohrs zu vergleichen und

liegen noch deutlich vor der Ausflugszeit der Fransenfledermäuse *(Myotis nattereri),* die ihr Quartier erst nach Einbruch der Dunkelheit verlassen.

Bei kleinen Fledermauskolonien begann der Ausflug relativ spät. Die Ursache dafür ist u.U. darin zu sehen, daß sich wenige, im Nistkasten einzeln hängende Tiere beim abendlichen Erwachen gegenseitig nur geringfügig stören, sich die Unruhe der ersten erwachenden Fledermaus also nicht oder nur wenig auf die anderen Individuen der Gruppe überträgt. In einem voll besetzten Nistkasten dagegen wird das erste unruhig werdende Tier auch die anderen Fledermäuse beeinflussen und in Kürze die gesamte Kolonie aus dem Tagesschlaf wecken, unabhängig von den verschieden synchronisierten inneren Uhren der Einzeltiere. In kurzer Folge hintereinander ausfliegende Tiere (‚Pulks') wechseln sich dann mit einzeln abfliegenden Fledermäusen ab. Swift (1980) sieht dafür drei mögliche Ursachen: 1. Pulkweises Ausfliegen ist das Ergebnis sozialer Stimulation, das Zeigen eines Verhaltensmusters durch ein Mitglied der Kolonie wirkt als Trigger für dasselbe Verhalten bei anderen Individuen und die Fledermäuse erregen sich so jeweils gruppenweise in Flugbereitschaft; 2. pulkweises Ausfliegen dient als Mittel zur Verwirrung von Freßfeinden; 3. die Fledermäuse jagen in Gruppen und warten am Ausflugloch auf andere zum Jagdflug bereite Individuen. Da die Bechsteinfledermäuse auch beim pulkweisen Ausfliegen das Quartier auf Grund der kleinen Fluglochöffnung immer einzeln verlassen müssen, wenn auch in kurzen Abständen von wenigen Sekunden, so scheint dieses Verhalten zur Verwirrung eines Freßfeindes nicht geeignet, da die Sicherheit einer ausfliegenden Fledermaus durch ein in kurzem Abstand vorausfliegendes Tier nicht erhöht wird. Ebenso ist unbekannt, ob die Bechsteinfledermäuse in Gruppen jagen; nach den bisherigen Beobachtungen ist dies eher unwahrscheinlich (unterschiedliche Abflugrichtung der Tiere vom Nistkasten).

Wenn das pulkweise Ausfliegen auf soziale Stimulation zurückgeführt werden kann, so sollten die Fledermäuse großer Kolonien deutlicher und ausgeprägter zur Pulkbildung neigen. Dies ist bei den Bechsteinfledermäusen auch tatsächlich der Fall. Während bei großen Wochenstubenkolonien Pulks ausfliegender Fledermäuse häufig 4 bis 6 (max. 9) Individuen umfaßten, verließen beim abendlichen Ausflug kleiner Kolonien (<15 Indiv.) viele Fledermäuse das Quartier allein; es bildeten sich zwischendurch nur kleine ‚Pulks' von 2 bis 3 Individuen.

Die Beobachtungen zeigten, daß ungünstiges Wetter, vor allem bei extremen Bedingungen, Einfluß auf den Ausflugsbeginn hat. Temperatureinbrüche verzögerten oder verhinderten den Ausflug der Bechsteinfledermäuse. Die von Laufens (1973b) bei tiefen Nachttemperaturen beobachtete deutliche Aktivitätsverkürzung bei *Myotis bechsteini* wird mit der vorliegenden Untersuchung bestätigt. Starke Regenfälle während der Ausflugszeit zeigten nur in einem Fall Auswirkungen auf das Ausflugsgeschehen: es bildeten sich vermehrt längere Pausen zwischen dem Ausflug einzelner Pulks.

Ähnliche Reaktionen auf ungünstige Witterungsbedingungen wurden z.B. von Engländer und Laufens (1968) für *Myotis nattereri,* von Böhme und Natuschke (1967) sowie von Gebhard und Ott (1985) für *Myotis myotis* und von v. Heerdt und Sluiter (1965) für *Nyctalus noctula* dargestellt.

Die nächtliche Aktivität vor dem Quartier ging mit zunehmendem Alter der Jungtiere bemerkenswert deutlich zurück. Da sendertragende adulte Bechsteinfledermäuse in der zweiten Augusthälfte während der Nacht das Tagesquartier nicht aufsuchten (Wolz 1986), sind die hohen Aktivitätswerte zwischen abendlichem Ausflug und morgendlicher Rückkehr vermutlich zum großen Teil auf Jungtiere zurückzuführen.

Fransenfledermäuse zeigen nach Laufens (1973a) ein den Bechsteinfledermäusen sehr ähnliches Verhalten mit einer bis Mitte August zunächst größer, dann allmählich kleiner werdenden Zahl von Individuen, die im Laufe der Nacht ins Quartier zurückkehren. Ab Mitte August bis Ende September werden auch bei *Myotis nattereri* nur wenige nächtliche Rückflüge ins Quartier aufgezeichnet.

In den Morgenstunden kehrten die Bechsteinfledermäuse zum Tagesquartier zurück, um es gruppenweise zu umfliegen. Durch dieses Verhalten lernen die Fledermäuse – vor allem die Jungtiere – Lage und Umgebung des Tagesquartiers genau kennen. Während der Zeit, in der die Tiere den Nistkasten noch in weiten Kreisen umflogen und minutenlang verschwanden, wurden vermutlich andere Ruheplätze überprüft. Zu diesem Zeitpunkt fällt dann die Entscheidung für das zukünftige Tagesquartier. Je mehr Individuen eine Gruppe bilden, desto mehr Information steht zur Auswahl eines optimal geeigneten Quartiers zur Verfügung.

60–40 min vor Sonnenaufgang herrschte beim morgendlichen Einflug die größte Aktivität vor dem Tagesquartier. Die Helligkeitswerte beim Einflug lagen dabei deutlich unter denen des Ausflugs, beim Erreichen des Helligkeitswertes von 1 lx (30 min vor SA) waren nahezu alle Fledermäuse ins Tagesquartier eingeflogen. Dies steht im Einklang mit LAUFENS (1972), der bei einzeln lebenden Männchen der Bechsteinfledermaus ebenfalls abends größere Flughelligkeiten als beim morgendlichen Einflug feststellte. Die Rückkehr der Tiere – nach seinen Beobachtungen zwischen der 60. und 20. min vor Sonnenaufgang – liegt im gleichen Zeitraum, der in der vorliegenden Untersuchung für Wochenstubenkolonien der Bechsteinfledermaus festgestellt wurde.

Danksagung

Mein besonderer Dank gilt Herrn Forstdirektor Dr. SPERBER und seinen Mitarbeitern im Forstamt Ebrach für ihre Unterstützung der Freilandarbeiten, Herrn G. SCHLAPP für das Überlassen von Beringungsunterlagen sowie Herrn Prof. Dr. O. v. HELVERSEN für kritische Durchsicht des Manuskriptes und hilfreiche Diskussionen. Der Fa. Gossen, Erlangen, gebührt mein Dank für die freundliche Überlassung von Helligkeitsmeßgeräten.

Zusammenfassung

Zur Registrierung der Aktivitäten von nistkastenbewohnenden Kolonien der Bechsteinfledermaus *(Myotis bechsteini)* wurde ein Infrarotlichtschranken-Ereignisspeicher entwickelt. Er besteht aus einem Lichtschrankenrahmen mit IR-Sender- und Empfängerelektronik, einer Auswerte- und Speichereinheit mit Echtzeituhr sowie Datendisplay und Ausgabesteuerung für Drucker oder Datenträger. Die Aufzeichnungen der Aktivitäten von Wochenstubenkolonien der Bechsteinfledermaus in 27 Beobachtungsnächten erbrachten folgende Resultate:

31–34 min nach Sonnenuntergang ist die Hälfte der Bechsteinfledermäuse ausgeflogen. Die Helligkeitswerte beim Ausflug der ersten Hälfte aller Tiere liegen zwischen 14 lx und 0,4 lx. 50 % der Individuen fliegen bei Helligkeiten unter 0,4 lx aus. Die Fledermäuse verlassen das Quartier am Abend in charakteristischer Weise: „Pulkweises Ausfliegen“. Sowohl die Koloniegröße wie auch extreme Wetterbedingungen (z.B. niedrige Temperaturen) beeinflussen Beginn und Verlauf des Ausflugs. Die nächtliche Aktivität vor dem Nistkasten nimmt mit dem Älterwerden der flugfähigen Jungtiere von Mitte August bis Anfang September deutlich ab. 110 min vor Sonnenaufgang beginnt der morgendliche Einflug der Fledermäuse. 60–40 min vor Sonnenaufgang herrscht die größte Aktivität vor dem Nistkasten, ca. 20 min vor Sonnenaufgang ist der Einflug beendet. Die Helligkeitswerte beim Einflug liegen unter denen des Ausflugs. Die an den Wochenstubenkolonien der Bechsteinfledermäuse gewonnenen Ergebnisse werden diskutiert und mit den Beobachtungen anderer Autoren verglichen.

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Z. Säugetierkunde 53 (1988) 267–275

ISSN 0044-3468

Distribution and biometry of *Sorex granarius* (Miller, 1910) (Soricinae: Insectivora)

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Receipt of Ms. 18. 5. 1987

Abstract

The area of distribution of *Sorex granarius* is confined to the Iberian Peninsula, including Galicia, the northern half of Portugal and the Central System. This species occupies forestal and supraforestal biotopes, with an altitudinal distribution from sea level to 2000 m.a.s.l. The interval of altitudes where this shrew is found is smaller and higher in the Central System (500–2000 m.a.s.l.).

Sorex granarius presents marked craniometric homogeneity, although there is a decremental tendency in size from north to south, the largest specimens occurring in Galicia.

Introduction

In the Iberian Peninsula, the shrews of the genus *Sorex* with sexual trivalent (*araneus-articus* group, Meylan and Hausser 1973, *araneus* group, Hausser 1976) are represented by three karyologically and biochemically well-characterized species: *Sorex araneus* Linnaeus, 1758; *Sorex coronatus* Millet, 1828; and *Sorex granarius* (Miller 1910).

Sorex granarius was described by Miller (1910) as a subspecies of *Sorex araneus* (*S. a. granarius*, terra typica La Granja, Segovia). Nonetheless, as a result of the karyological and morphological analysis by Hausser et al. (1975), the form *granarius* was raised to species rank.

In 1914, Cabrera attributes a specimen from Vilaboa (La Coruña) to this form and postulates that the distribution of *granarius* is the central and northwestern Iberian Peninsula. Later, various authors report the species in Galicia (Heim de Balsac and de Beaufort 1969; Nores 1979; Lopez-Fuster 1983), the Central System (Hausser et al. 1975; Campos 1977; Catzeflis et al. 1982; Arenas 1983; Catzeflis 1984; Hausser 1984) and Portugal (Niethammer 1970; Madureira and Magalhaes 1980); Madureira and Ramalinho 1981; Ramalinho, in press). The references by Almaça (1968) and Garzon-Heydt et al. (1971) to *Sorex araneus* in Portugal and the Central System, respectively, in reality correspond to *Sorex granarius*. In contrast, the specimens from Villarreal (Alava) that Malec and Storch (1964) consider *Sorex granarius* should be referred to *Sorex coronatus* (Hausser et al. 1975).

As for *Sorex* from northern Burgos (Sedano), bibliographic findings are contradictory. According to Niethammer (1956), these specimens pertain to *Sorex granarius* in the light of their coloring and dimensions, while Garzon-Heydt et al. (1971) assign them to *Sorex araneus* (read *coronatus*). On the basis of Hausser's (1984) multivariate analysis, the specimens from Sedano are *Sorex granarius*. Nonetheless, Hausser indicates that this diagnosis must be erroneous according to the geographical distribution of *Sorex granarius* and *Sorex coronatus*. In the map of distribution described by Hausser et al. (1985), the specific affiliation of these specimens is not mentioned.

The objective of our paper was to establish the morphometric features of *Sorex granarius* and offer our biogeographical findings.

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Material and methods

Material analysed

Two hundred thirty-five specimens were studied. The material came from the scientific collections of: the Unidad de Zoologia Aplicada, deposited at El Encin, Alcalá de Henares; the Department of Vertebrates of the School of Biology, Universidad Central de Barcelona; and the Department of Vertebrates of the School of Biology, Universidad de Salamanca.

The specific determination was realized on the basis of the cranial criteria proposed by Miller (1912) and Hausser et al. (1975). For the captured material, also was examined the coloration and body measurements (see Cabrera 1914).

Specimens captured: Madrid: Alto de Guarramillas, 1. Segovia: Puerto de Fuenfria, 1. Avila: Laguna de El Barco, 1. León: Lago de la Baña, 1. La Coruña: Vallegestoso, 1; Ferrol, 1. Lugo: San Ciprián, 2.

Owl pellet material: Segovia: Grado del Pico, 1 skull and 2 mandibles; Riofrío de Riaza, 9 skulls and 9 mandibles. Avila: El Barco de Avila, 75 skulls and 54 mandibles. Cáceres: Hervás, 3 skulls and 3 mandibles; Baños de Montemayor, 1 skull and 1 mandible; Acebo, 1 skull and 1 mandible. Salamanca: Villasrubias, 1 skull and 1 mandible; Candelario, 16 skulls and 13 mandibles. La Coruña: Arines, 1 skull and 1 mandible; Brandomil, 6 skulls and 3 mandibles; Puebla de Caramiñal, 2 mandibles; Montfero, 1 skull and 2 mandibles; Pontedeume, 7 skulls and 2 mandibles. Orense: Castrocaldelas, 5 skulls and 6 mandibles.

Body, skull and jaw measurements

We used the following measurements: CC = head + body length. C = tail length. P = hind foot length. O = ear length. Peso = weight in grams. LCI = condyle-incisor length. LCB = condyle-basal length. LR = rostral length. LCC = length of skull case. LSB = staphylion-basion length. AIO = interorbital width. AZ = zygomatic width. ACC = skull case width. SDS = length of upper dental series. P^4–M^3 = P^4–M^3 length. α = labial length of the mandible. β = length of articular process. γ = inclination of the coronoid process. δ = mandibular foramen. LIA = incisor-angle length. LM = mandibular length. LFT = length of internal temporal fossa. SDI = length of lower dental series. M_1–M_3 = M_1–M_3 length. LM_3 = maximum M_3 length, LA = articular length of mandible. HC = coronoid height (Fig. 1).

The cranial measurements and mandibular LA and HC were realized with a Mitutoyo caliper, $\pm$ 0.02 mm precision. For the other mandibular measurements, a "Reichert Mak MS" stereomicroscope ocular micrometer was used. The precision of this instrument, by lens, was: 1:1 lens, $\pm$ 0.065 mm (α, LIA, LM, SDI, M_1–M_3); 1:4 lens, $\pm$ 0.015 mm (β, γ, LFT, LM); 1:10 lens, $\pm$ 0.006 mm (δ). We used the method described by Sans-Coma (1979) for the measurements with stereomicroscope, which is inspired by that proposed by Hausser and Jammot (1974), based on use of the "bloc comparateur optique" conceived by Jammot (1973).

Biomathematical analyses

Data were processed with an IBM 3083/XE01 computer of the Calculation Center of the University of Barcelona. Sample means were compared by variance analysis – ANOVA – and paired samples by the Tukey method. The degree of intersample affinity for each variable was evaluated by the Student-Newman-Keuls test (Dixon 1983: BMDP program p7D).

Results and conclusions

Distribution and habitat

Sorex granarius is distributed throughout the Central System, from Sierra de Ayllón (Spain) to Serra da Estrela (Portugal), extending throughout Portugal from north of the "Tajo" River to Galicia (Fig. 2).

In the Central System, the species is located at altitudes between 500 and 2000 meters, occupying the supra- and oromediterranean bioclimatic levels (Rivas-Martinez 1981, 1983). In this area, where captures were scant, *Sorex granarius* was found especially in forest biotopes: woods of *Fagus sylvatica* (Cantalojas), *Pinus silvestris* (Balsain, Hoyos del Espino), *Quercus pyrenaica* (Candelario) and *Quercus rotundifolia* (La Maya). *Sorex granarius* also occupies cultivated lands that replace authocthonous forests, like green

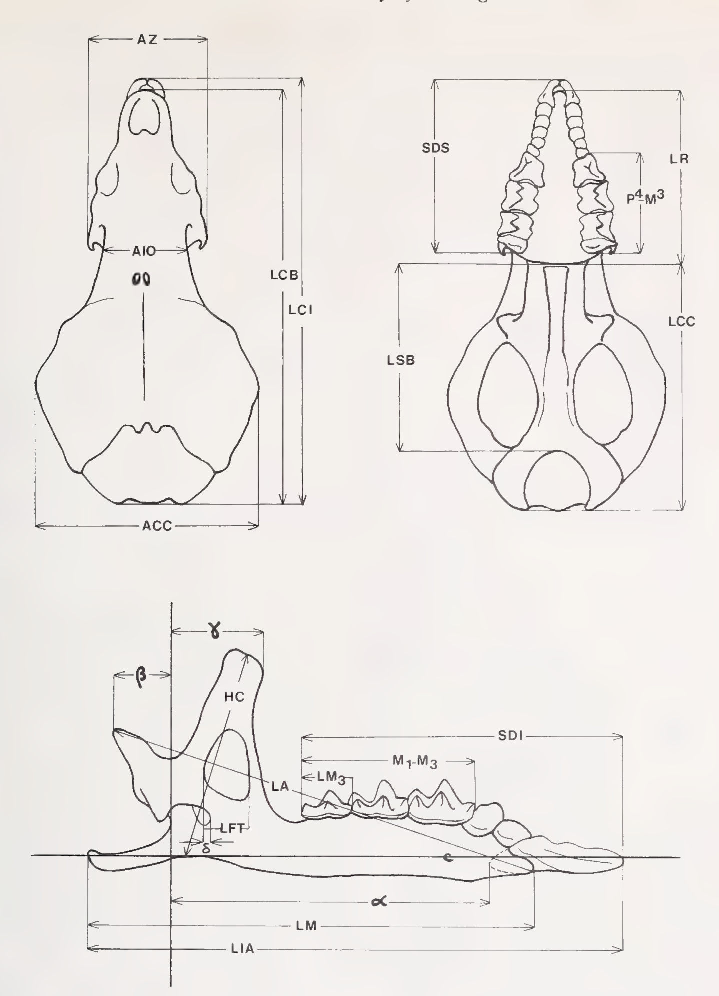
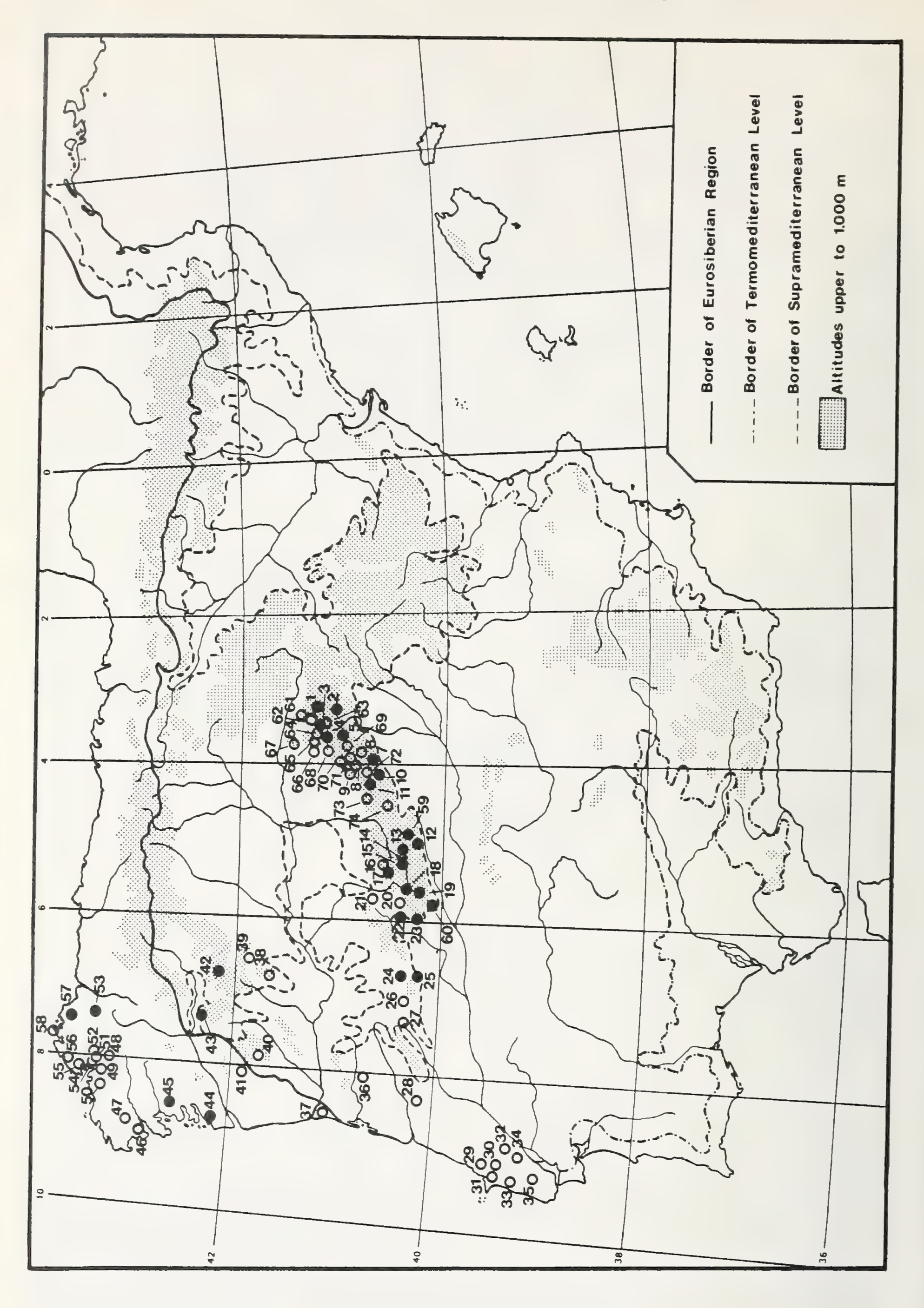


Fig. 1. Cranial and mandibular measurements of *Sorex granarius*

gardens (El Barco de Avila) and forests of *Castanea sativa* (Hervás) and *Pinus pinaster* (Villasrubias). Above the forest level, the species was captured in granite rock falls adjacent to areas of *Nardus stricta* (Laguna de El Barco, Galayos). From the western extreme of the Central System, the distribution of *Sorex granarius* is at progressively lower altitudes, appearing at the mesomediterranean level and reaching the coast of Portugal and Galicia. According to Madureira and Ramalinho (1981), the species is present in Portugal in almost all the biotopes with a bushy stratum, being more abundant in densely vegetated, relatively humid terrain. In northern Portugal, *Sorex granarius* introduces itself into the eurosiberian region, penetrating in Galicia, where it occupies the *Quercus pyrenaica* woods and areas where the natural forest has been replaced by *Eucaliptus* and *Pinus pinaster* plantations.

Generally speaking, the territories occupied by *Sorex granarius* are characterized by mean annual temperatures of 3–15 °C with cold to extremely cold winters and mean annual precipitation in excess of 600 mm.


Border of Eurosiberian Region
Border of Termomediterranean Level
Border of Suprameditarranean Level
Altitudes upper to 1.000 m



Biometry

The origin of the material, predominantly from owl pellets, precludes our establishing the somatometric and biological characteristics of *Sorex granarius*. Nonetheless, since the bibliographic data on these aspects are restricted to those communicated by MILLER (1912), we consider it interesting to offer the body measurements obtained in 10 specimens from diverse localities (Table 1).

Table 1. **Body measurements of *Sorex granarius***

Locality	Date	Sex	CC	C	P	O	Weight
Balsain (Segovia)	23. 04. 1977	♀	64.0	39.0	12.0	7.4	–
Alto de Guarramillas (Segovia)	—	♀	51.0	37.0	12.0	6.4	6.0
Laguna de El Barco (Avila)	23. 06. 1984	♀	51.0	38.0	12.0	7.6	8.1*
Gontán-Quende (Lugo)	23. 07. 1979	–	50.0	36.0	11.0	5.6	–
Vilas, S. Ciprián (Lugo)	11. 08. 1978	–	61.0	41.0	12.0	6.9	7.5
S. Ciprián (Lugo)	26. 07. 1976	–	61.0	39.0	12.0	7.1	6.5
Ferrol (Coruña)	24. 09. 1973	–	63.0	40.0	12.0	7.6	–
Ferrol (Coruña)	24. 09. 1973	–	58.0	41.0	12.0	7.3	–
Vallegestoso (Coruña)	30. 05. 1976	♀	65.5	46.0	12.0	5.3	–
El Barco de Avila (Avila)	29. 08. 1987	♀	68.0	39.0	11.5	6.0	6.5

* = weight corresponding to a pregnant female

Moreover, in view of the fragmentary nature of craniometric information, we list in Table 2 the values of cranial variables obtained in our specimens from Galicia (the data from Gredos and Guadarrama are insufficient). Our findings concur with those communi-

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Fig. 2. Distribution of *Sorex granarius* in the Iberian Peninsula. Black circles: own data. White circles: references in literature. 1: Grado del Pico (Segovia), 2: Cantalojas (Guadalajara), 3: Riofrío de Riaza (Segovia). 4: Cerezo de Arriba (Segovia), 5: Pto. de Somosierra (Madrid), 6. Rascafría (CATZEFLIS et al. 1982). 7: Alto de Guarramillas (Madrid), 8: Balsaín (GARZON et al. 1971), 9: La Granja (MILLER 1910). 10. Cercedilla (Madrid), 11: Pto. de Fuenfría (Segovia), 12: Galayos (Avila), 13: Barajas (Avila), 14: Hoyos del Espino (Avila), 15: Navalperal de Tormes (Avila), 16: Piedrahita (HAUSSER 1984), 17: Santiago del Collado (Avila), 18: El Barco de Avila (Avila), 19: Laguna de El Barco (Avila), 20: Candelario (HAUSSER et al. 1975), 21: La Maya (CAMPOS 1977), 22: Baños de Montemayor (Cáceres), 23: Hervás, (Cáceres), 24: Villasrubias (Salamanca), 25: Acebo (Cáceres), 26: Sabugal (MADUREIRA and MAGALHAES 1980), 27: Belmonte (MADUREIRA and RAMALINHO 1981), 28. Miranda do Corvo (MADUREIRA and RAMALINHO 1981), 29: Caldas da Rainha (MADUREIRA and RAMALINHO 1981), 30: Obidos (RAMALINHO in press), 31: Serra d'El Rei (RAMALINHO in press), 32: Rio Maior (NIETHAMMER 1970), 33: Lourinhã (RAMALINHO in press), 34: Epinera-Cercal (NIETHAMMER 1970), 35: Tapada de Mafra (MADUREIRA and RAMALINHO 1981), 36: Torredeira (RAMALINHO in press), 37: Grijo (RAMALINHO in press), 38: Serra da Nogueira (RAMALINHO in press), 39: Cernadilla (HAUSSER 1984), 40: Cabeceiras de Basto (MADUREIRA and MAGALHAES 1980), 41: Géres (MADUREIRA and RAMALINHO 1981), 42: Lago de la Baña (León), 43: Panjón-Nigrán (Pontevedra), 44: Castrocaldelas (LOPEZ-FUSTER 1983), 45: Caldas de Reyes (Pontevedra), 46: Puebla del Caramiñal (LOPEZ-FUSTER 1983), 47: Brandomil (LOPEZ-FUSTER 1983), 48: Montesalgueiro (NORES 1979), 49: Betanzos (NORES 1979), 50: Vilaboa (CABRERA 1914), 51: Pontedeume (LOPEZ-FUSTER 1983), 52: Caaveiro (NORES 1979), 53: Gontán-Quende (Lugo), 54: Montfero (LOPEZ-FUSTER 1983), 55: Ferrol (NORES 1979), 56: Lagoa (NORES 1979), 57: San Ciprián (Lugo), 58: Estaca de Bares (NORES 1979), 59: San Esteban del Valle (Avila), 60: Monasterio de Yuste (Cáceres), 61: Estebanvela (ARENAS 1983), 62: Villacorta (ARENAS 1983), 63: Pto. de la Quesera (ARENAS 1983), 64: Riaza (ARENAS 1983), 65: Sequera de Fresno (ARENAS 1983), 66: Encinas (ARENAS 1983), 67: Valdevacas (ARENAS 1983), 68: Sotillo (ARENAS 1983), 69: Gallegos (ARENAS 1983), 70: da Cuesta (ARENAS 1983), 71: Sotosalbos (ARENAS 1983), 72: Peñalara (ARENAS 1983), 73: Revenga (ARENAS 1983), 74: El Espinar (ARENAS 1983)

Table 2. Values of descriptive statistics of cranial variables in *Sorex granarius* from Galicia

	n	$\bar{x}$	s	Σx^2	min.	max.
LCI	2	18.2	0.1	663	18.1	18.3
LCB	4	17.7	0.1	1246	17.5	17.8
LR	23	7.5	0.2	1285	7.2	7.8
LCC	5	10.2	0.2	516	9.9	10.4
LSB	5	8.0	0.3	317	7.6	8.3
AIO	22	3.8	0.1	317	3.5	4.1
AZ	13	5.3	0.1	363	5.1	5.4
ACC	3	8.7	0.4	229	8.3	9.0
SDS	10	7.7	0.2	590	7.3	7.9
P^4–M^3	19	4.3	0.1	353	4.1	4.5

Table 3. Values of descriptive statistics of jaw measurements of *Sorex granarius* from Galicia (GA), Gredos (GR) and Guadarrama (GU)

		n	$\bar{x}$	s	Σx^2	min.	max.
	GA	20	6.3	0.2	793	5.80	6.72
α	GR	73	6.3	0.2	2901	5.80	6.59
	GU	13	6.1	0.1	486	5.93	6.33
	GA	20	1.2	0.1	27	1.00	1.29
β	GR	73	1.1	0.1	96	0.87	1.29
	GU	13	1.1	0.1	16	0.94	1.26
	GA	20	1.9	0.2	72	1.52	2.23
γ	GR	73	1.9	0.1	256	1.51	2.29
	GU	13	1.9	0.2	49	1.68	2.26
	GA	20	0.2	0.1	1	0.04	0.37
δ	GR	73	0.2	0.1	3	0.00	0.41
	GU	13	0.1	0.1	0	0.00	0.38
	GA	15	11.7	0.2	2058	11.33	12.13
LIA	GR	60	11.4	0.3	7832	10.94	11.99
	GU	10	11.3	0.3	1276	10.94	11.60
	GA	15	9.6	0.2	1387	9.36	10.02
LM	GR	64	9.5	0.3	5791	9.09	10.15
	GU	10	9.4	0.2	886	9.23	9.62
	GA	15	7.2	0.2	774	6.85	7.38
SDI	GR	58	6.9	0.2	2764	6.33	7.25
	GU	11	6.9	0.2	522	6.59	7.25
	GA	20	1.0	0.1	21	0.90	1.16
LFT	GR	73	1.0	0.1	75	0.78	1.23
	GU	13	1.0	0.1	12	0.81	1.13
	GA	16	3.7	0.1	219	3.56	3.82
M_1–M_3	GR	62	3.6	0.1	810	3.43	3.95
	GU	11	3.6	0.1	144	3.56	3.82
	GA	16	1.0	0.0	16	0.94	1.07
LM_3	GR	55	1.0	0.0	55	0.94	1.10
	GU	11	1.0	0.0	11	0.97	1.07
	GA	20	9.1	0.3	1661	8.70	9.60
LA	GR	71	9.1	0.2	5816	8.60	9.50
	GU	13	9.1	0.2	1070	8.80	9.40
	GA	20	4.3	0.2	369	4.00	4.60
HC	GR	73	4.2	0.1	1309	3.90	4.60
	GU	13	4.3	0.2	236	4.00	4.50

Table 4. **Individual comparison between paired samples for each analysed variable, according to Tukey's method**

	GA–GR	GA–GU	GR-GU				
				GU	GA	GR	
α	0	<0.05	<0.01	6.11	6.29	6.30	$\bar{x}$
				13	20	73	n
				GU	GR	GA	
β	0	0	0	1.09	1.14	1.15	$\bar{x}$
				13	73	20	n
				GR	GA	GU	
γ	0	0	0	1.87	1.89	1.93	$\bar{x}$
				73	13	20	n
				GU	GA	GR	
δ	0	0	0	0.14	0.19	0.19	$\bar{x}$
				13	20	73	n
				GU	GR	GA	
LIA	<0.01	<0.01	0	11.29	11.42	11.71	$\bar{x}$
				10	60	15	n
				GU	GR	GA	
LM	0	0	0	9.41	9.51	9.63	$\bar{x}$
				10	64	15	n
				GU	GR	GA	
SDI	<0.01	<0.01	0	6.89	6.90	7.18	$\bar{x}$
				11	58	15	n
				GU	GR	GA	
LFT	0	0	0	0.97	1.01	1.02	$\bar{x}$
				13	73	20	n
				GR	GU	GA	
M_1–M_3	<0.01	0	0	3.61	3.62	3.70	$\bar{x}$
				62	11	12	n
				GR	GA	GU	
LM_3	0	0	0	1.00	1.01	1.02	$\bar{x}$
				55	16	11	n
				GR	GU	GA	
LA	0	0	0	9.05	9.07	9.11	$\bar{x}$
				71	13	20	n
				GR	GU	GA	
HC	0	0	0	4.23	4.26	4.29	$\bar{x}$
				73	13	20	n

Results of Student-Newman-Keuls multiple test of rank for Galicia (GA), Gredos (GR) and Guadarrama (GU). 0 = Not significant differences

cated by Miller (1912), Hausser et al. (1975), Madureira and Magalhaes (1980), Nores (1979) and Ramalinho (1981).

Table 3 shows the statistics for the descriptive mandibular parameters of the Galicia, Gredos and Guadarrama samples. Comparison of the sample means (ANOVA test) discloses notable biometric similarity among populations. Significant differences were detected only in α ($F = 6.24$, $p < 0.01$), LIA ($F = 8.71$, $p < 0.01$), SDI ($F = 10.30$, $p < 0.01$) and M_1–M_3 ($F = 4.76$, $p < 0.01$).

Individual comparisons between pairs of samples (Table 4) also confirm the scant divergence of peninsular *Sorex granarius* populations. Between the populations of Galicia

and Gredos, we only found statistically significant differences in LIA ($p < 0.01$), SDI ($p < 0.01$) and M_1–M_3 ($p < 0.01$). Between the Galicia and Guadarrama samples, the most marked divergences were in α ($p < 0.05$), LIA ($p < 0.01$) and SDI ($p < 0.01$). Between Gredos and Guadarrama, there was an even greater degree of biometric similarity, only α showing significant differences ($p < 0.01$).

In view of the mean values obtained for all these populations (see Table 3), the specimens from Galicia generally evidence the largest mandibular dimensions, although these differences lack statistical significance (observe values of β, LIA, LM, SDI, LFT, M_1–M_3, LC and HC). Due to their biometrical similarity, the relationship between the sizes of the Gredos and Guadarrama samples has not been completely defined.

To determine the degree of intersample affinity in each parameter, mean values were processed by the Student-Newman-Keuls test. In the graphic representation of results (Table 4), the populations with mean values not significantly heterogeneous are underlined (Sokal and Rohlf 1979). The resulting diagrams evidence the close relationship among the populations analysed. The only variable to statistically separate the Guadarrama population was α, which was smaller in this sample. The specimens from Galicia differ from Gredos and Guadarrama in LIA, SDI and M_1–M_3, the mean values of these parameters being higher in the Galicia samples.

On the basis of these findings, although there was no evidence of intraspecific mandibular biometric differences in *Sorex granarius*, there was a general tendency to smaller size from north to south. It is interesting to point out that in the Iberian Peninsula, *Crocidura russula* and *Crocidura suaveolens* have been found to present a clinal variation consisting in progressive reduction of cramiometric values to the south (Rey and Landin 1973; Rey and Rey 1974; Sans-Coma et al. 1987).

Acknowledgements

We are grateful to M. Navarro and Dr. V. Perez-Mellado, who contributed 7 specimens and six new localities, as to Dr B. Thomas, who translated this manuscript to English, and I. Maier for translating to German.

Zusammenfassung

Verbreitung und Biometrie von Sorex granarius (Miller, 1910) (Soricinae: Insectivora)

Die Verbreitung von *Sorex granarius* ist auf die Pyrenäen-Halbinsel beschränkt. Hier ist diese Art in Gallizien, der nördlichen Hälfte von Portugal und im Zentralgebirge anzutreffen. *Sorex granarius* bewohnt vorwiegend Waldgebiete. Die vertikale Verbreitung erstreckt sich von der Meereshöhe bis zur Höhe von 2000 m. Im Zentralgebirge ist dieses Intervall kleiner (500–2000 m). Die Biometrie der Schädel von untersuchten Individuen ist sehr gleichartig, obwohl sich eine Tendenz zur Größenabnahme von Norden nach Süden beobachten läßt. Die größten Schädel wurden in Gallizien gefunden.

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Z. Säugetierkunde 53 (1988) 276–280

ISSN 0044-3468

Notes on some bats from northern Thailand, with comments on the subgeneric status of *Myotis altarium*

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Receipt of Ms. 06. 04. 1987

Abstract

Reported is the occurance of four species of bats from extreme northern Thailand collected by members of the National Speleological Society, USA, Thailand Karst Hydrologic Expedition. Single specimens of *Aselliscus stoliczkanus, Ia io, Miniopterus macrodens*, and *Myotis altarium* were collected. This is the first record of *M. altarium* outside of China and only the second record for *I. io*. Although known from the area, our specimen of *A. stoliczkanus* does not match published color patterns of this species from Thailand. We provide the first published photograph of the skull of *M. altarium* and an expanded description of this species because previously published descriptions are inadequate to place this species at the subgeneric level. We compared *M. altarium* directly to members of three other subgenera of *Myotis* and conclude it belongs in the subgenus *Myotis*.

Introduction

The Thailand Karst Hydrologic Survey, fielded by members of the National Speleological Society between December 1983 and February 1984, provided several specimens of cave-dwelling bats from the limestone mountains of extreme northern Thailand. We report here three species of Vespertilionidae plus one species of Hipposideridae. We found published descriptions of one of the species collected, *Myotis altarium*, inadequate to properly place it at the subgeneric level. Therefore, we present an expanded description of *M. altarium*, as well as, the first photographs of its skull. Specimens have been deposited in the mammal collection of the Natural History Museum of Los Angeles County (LACM). The rhinolophids collected during this expedition are reported separately (McFarlane and Blood 1986).

Results and discussion

Systematic accounts

Aselliscus stoliczkanus Dobson, 1871 (Hipposideridae)

Specimen collected; LACM 70301; collected by R. Hemperly, 24 Dec. 1983; male, in alcohol with skull extracted. Northern Thailand; Chang Dao Mountain, Chang Dao Cave. 19°23′N, 98°54′E. Some selected measurements (in mm) are head and body length, 43; tail length, 38; forearm length, 41; greatest length of skull, 18; hind foot length, 5; ear length, 8. Lekagul and McNeeley (1977) report this species to be uncommon, but wide spread. They further report that this species occurs in two color phases, a brown-gray phase and a yellow-red phase. The LACM specimen has long dorsal fur (7 mm) which is a creamy white at its base with rich dark brown tips. The ventral fur color is a silvery brown.

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Miniopterus macrodens Maeda, 1982 (Vespertilionidae)

Specimen collected: LACM 70323; collected by R. HEMPERLY 12 Jan. 1984; male, in alcohol with skull extracted. Northern Thailand, Aung Kang Region, Big House Cave; 19°50′N, 99°10′E. Selected measurements (in mm) are as follows; total length, 107; forearm length, 50.5; greatest length of skull, 16.4; ear length 16; tragus length, 4.5; length of third metarcarpal, 47.5; length of first phalanx of digit 3, 11.9; length of second phalanx of digit 3, 34.5. Our specimen is all black in color including the flight membranes. This species is part of the *M. maginater* group (R. PETERSON, pers. comm.)

Ia io Thomas, 1902 (Vespertilionidae)

Specimen collected: LACM 70321; collected by R. HEMPERLY 11 Jan. 1984; in alcohol. Northern Thailand, Aung Kang Region, Big House Cave. 19°50′N, 99°10′E. Some representative measurements (in mm) include head and body length, 90.6; tail length, 71.5; forearm length, 75.3; ear length, 26; tragus length, 8.5; length of metacarpal III, 68.3; length of third phalanx of digit III, 11.9. This specimen was collected by hand near the entrance of Big House Cave. The field notes indicate that it was not in the immediate company of other bats. However, three other species were collected in this same cave: *Rhinolophus malayanus, R. robinsoni*, and *M. altarium* (MCFARLANE and BLOOD 1986). Only one other specimen (Museum of Comparative Zoology 3549) is known from northern Thailand, near Chang Dao (ALLEN and COOLIDGE 1940).

Myotis altarium Thomas, 1911 (Vespertilionidae)

Specimen collected: LACM 70234, collected by J. BENEDICT 19 Jan. 1984; Northern Thailand, Aung Kang Region, Big House Cave; male, in alcohol with skull extracted. This single specimen was collected approximately one meter above a stream, on the cave wall. The field notes do not indicate whether or not this specimen was near other bats. This specimen represents the first record for this species outside of mainland China and extends the known range for this species by 1250 km southwest. The two other known localities are Omi San, Szechwan Province, China (the type locality) and 3 mi. east of Kweiyang City in Kweichow Province, China (STAGER 1949). Two of STAGER's six specimens (LACM 8214 and 8215) compare favorably with the new specimen. Selected measurements of LACM 70234, 8214, 8215, and the type (as given by THOMAS 1911) respectively are as follows: head and body length, 55, 60, 58, 55; forearm length, 44, 45.35, 42.90, 45; tibia, 16.50, 18.65, 18.10, 29 (reported as lower leg plus foot), hindfoot length, 11, 12, 12, none repoted for type, ear length, 22, 24, 24, 22; greatest length of skull, 15.50, 15.95, 16, 15.2.

In addition to *M. altarium*, seven other species of *Myotis* are known from northern Thailand (LEKAGUL and MCNEELY 1977): *M. mystacinus, M. annectans, M. rosseti, M. siligorensis, M. horsfieldii, M. chinensis*, and *M. hasseltii*. Published information on the relationships of *M. altarium* are contradictory because so little material is available.

THOMAS (1911) stated that the morphology of *M. altarium* most resembled *M. pequinus*, a member of the large footed subgenus, *Leuconoe*. TATE (1941) placed *M. altarium* in the *M. emarginatus* section of the subgenus *Selysius*. The other species in this section of *Selysius* (sensu TATE 1941) are *M. emarginatus, M. peytoni* (= *montivagus*; HONACKI et al. 1982), *M. primula* (= *annectans*; HONACKI et al. 1982), and *M. saturatus* (= *emarginatus*; CORBET 1978). FINDLEY (1972) also placed *M. altarium* in the subgenus *Selysius*, but this analysis placed *M. altarium* close to a different group of species: *M. mystacinus, M. siligorensis, M. davidii* (= *mystacinus*; HONACKI et al. 1982), and *M. ikonnikovi*, FINDLEY's (1972) analysis and later classification placed the species *M. emarginatus* and *M. pequinus* into the subgenus *Myotis*. The relationships of *M. altarium* are

therefore confused, because according to TATE (1941) it should be placed close to *M. emarginatus* and so should be in the subgenus *Myotis* as this subgenus is characterized by FINDLEY (1972).

Based upon the three LACM specimens and THOMAS (1911), *M. altarium* can be characterized as follows: a medium sized *Myotis* with ears twice as long as they are wide, and which are distinctively black and translucent. The lateral edge of the ears are folded cranially. When laid forward the ears reach 5 mm beyond the tip of the muzzle. There is a distinct lobule at the base of the ear. The lobule is separated from the ear by a deep notch. The tragus is long, thin, and bluntly pointed. The flight membranes are naked, blackish brown in color and attach to the hind foot at the distal end of the metatarsal of digit one. There are eight striae on the uropatagium, which is naked dorsally, but with scattered hairs ventrally. The dorsal fur is light brownish in color and 12–15 mm in length. The ventral fur color is lighter having dark bases and whitish tips. The calcar is weakly lobed at its mid point. The hind foot measures over 60% of tibial length.

The skull of *Myotis altarium* (Fig. 1) has a short and distinctly upturned rostrum in lateral view. A line drawn along the long axis of the rostrum intersects a line drawn along the long axis of the cranium at approximately 145°. The skull slopes sharply anteriorly to a point above the posterior premolars. The skull profile has a slight convexity at mid-braincase (where the frontal and parietal bones meet). The nasal bones are flattened proximally and slightly arched (lateral to medial) distally and curved upwards distally at the premaxillary-nasal junction. The junction of the premaxillary-nasal bones is at the level of the superior surface of the orbit. The posterior part of the premaxillary bones are arched and display a obvious bump in lateral view. The zygomatic arches are consistant in depth, as seen in lateral view and expand somewhat posteriorly in dorsal view. The anteorbital foramen opens 0.7 mm anterior to the orbit above the anterior labial root of P^3 and is 0.3 mm in diameter. The anteorbital foramen leads to an enclosed basin found above the roots of the premolars.



Fig. 1. Dorsal, lateral, and ventral views of the cranium of *M. altarium.* (Approximately 3× life size)

The ventral skull surface displays several distinctive features. The palate is deeply vaulted. An unusual feature of the palate is a sharp ridge running transversely between the canine teeth. The foramen ovale is large and conspicuous in ventral view. The basisphenoid is raised above the floor of the interbullar area resembling a bridge. There is no sagittal crest on any of the specimens. All upper and lower premolars are fully in line with the

toothrow. The dental formula is 2/3-1/1-3/3-3/3. The ratio of the length to width of the M^3 is 1:3. The crown of the M^2 is characterized by not possessing a ridge connecting the hypocone and metacone. Because of the orientation of the rostrum the incisors and canines are directed obliquely anteriorly.

We have examined both TATE (1941) and FINDLEY (1972) in compiling a provisional list of characteristics of these three subgenera of *Myotis*. Although it is not within the scope of this paper to attempt to fully characterize all the subgenera of the genus *Myotis* we briefly list some of the most important characteristics of the subgenera needed to evaluate *M. altarium.*

M. altarium is not a member of the large-footed subgenus *Leuconoe* because it does not possess a protoconule on its upper molars, a key characteristic of this subgenus (TATE 1941). Species within the subgenus *Selysius* possess at least the following: small feet (< 50 per cent of the tibia length), wing membrane to base of first toe, calcar with lobe, ear small, low rostrum with abruptly rising frontal region, length to width ratio of M^3 is 0.8 to 1.5, small overall size, large uropatagial traps, uropatagial hairs restricted to striae, anteorbital foramen diameter near 0.6 mm. The species included within the subgenus *Myotis* possess at least the following: large species with the feet not enlarged (hind foot at least 60 per cent of tibia length), ears can be elongate, broadened or both, rostrum is low with a gradually rising frontal region, uropatagium nearly naked with hairs scattered widely over its surface not restricted to striae, length to width ratio of M^3 is 1 to 2.7, anteorbital foramen is close to orbit.

In order to best compare the above characteristics to *M. altarium* we examined members of each subgenus and compared them directly to *M. altarium* (see specimens examined). The dorsal skull profile and the longitudinal sulcus between the nasal bones in *M. altarium* are intermediate between *M. myotis* and *M. muricola*. This sulcus is deep in *M. emarginatus* and *M. muricola* and essentially missing in *M. myotis*. The structure of the zygomatic arches, crown pattern of M^2, disposition of the anteorbital foreamen, distribution of uropatagial hair, attachment of the wing to the foot, length to width ratio of M^3, relative length of its hind foot, and ear structure most closely resemble the condition of the subgenus *Myotis*.

In conclusion, based upon the comparisons we have made *M. altarium* is best considered closest to the subgenus *Myotis*, but our comparison has been too narrow to place *M. altarium* close to any one species of *Myotis*.

Specimens examined

Myotis altarium (3); LACM 70234, 8214, 8215, localities in text: *Myotis emarginatus* (5); LACM 58397–58401, Portugal: *Myotis thysanodes* (1); LACM 55951, Colima, Mexico: *Myotis daubentoni* (1); LACM 58781, Germany: *Myotis muricola* (6); American Museum of Natural History (AMNH) 102967–102972, Sumatra: *Myotis myotis* (6); AMNH 150102–150107, Bavaria, Germany.

Acknowledgements

We would like to thank the members of the Karst Hydrologic survey team, especially B. BENEDICT and R. HEMPERLEY for collecting and donating the specimens upon which this report is based. D. PATTEN, J. MATSON, L. BARKELY, and S. GEORGE read early versions of the manuscript and provided helpful comments and discussion. We wish to thank K. KOOPMAN and M. BOGAN for thoughtfully reviewing the manuscript. We are very grateful to R. PETERSON who identified the specimen of *Miniopterus*. Many thanks also go to C. BLOOD for reading and proofing the many versions of this work. The photographic work was performed by J. DELEON and D. MEIER and the figure was prepared by C. MALOOF of the Natural History Museum of Los Angeles County. We are grateful to I. KRATTIGER who translated the summary.

Zusammenfassung

Über einige Fledermäuse aus dem nördlichen Thailand mit Bemerkungen zur subgenerischen Zugehörigkeit von Myotis altarium

Über folgende, im äußersten Norden Thailands Ende 1983 bis Anfang 1984 gesammelten Fledermausarten wird berichtet: *Aselliscus stoliczkanus, Ia io, Miniopterus macrodens* und *Myotis altarium.* Unser Exemplar von *Myotis altarium* bildet den ersten Nachweis dieser Art außerhalb Chinas. Wie eine ausführliche Beschreibung ergibt, dürfte *M. altarium* in die Untergattung *Myotis* der Gattung *Myotis* gehören.

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Z. Säugetierkunde 53 (1988) 281–293

ISSN 0044-3468

Search calls of echolocating *Nyctalus leisleri* and *Pipistrellus savii* (Mammalia: Chiroptera) recorded in Switzerland

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Receipt of Ms. 06. 04. 1987

Abstract

Studied the search calls of hunting *Nyctalus leisleri* and *Pipistrellus savii* north and south to the Swiss Alps.

The ultrasounds were converted to audio frequencies by a 8:1 dividing detector and subsequently analysed in the laboratory on a dual channel digital oscilloscope using a period meter.

In both species single harmonic pulses with shallow frequency modulation and pulses of constant frequency were recorded.

Search pulses of *N. leisleri* (median values of 204 signals): pulse duration 9.2 ms; start frequency 25.1 kHz; center frequency 24.3 kHz; end frequency 23.7 kHz; sweep bandwidth 1.6 kHz. The intervals (N = 2153) between search pulses followed a bimodal distribution with a higher mode at 243 ms and a weaker one at 350 ms.

Search pulses of *P. savii* (median values of 236 signals): pulse duration 12.1 ms; start frequency 34.2 kHz; center frequency 32.8 kHz; end frequency 32.0 kHz; sweep bandwidth 2.2 kHz. The intervals (N = 1341) between search pulses followed a bimodal distribution with a higher mode at 192 ms and a weaker one at 294 ms.

In both species various signal variables were significantly correlated. In addition to echolocation signals two types of social calls of *N. leisleri* were recorded. The first type consisted of a group of 4 pulses ranging from 38–16 kHz. The second type was a single, linear period modulated pulse of 20–27 ms duration, ranging from 21–10 kHz.

Introduction

In the course of a study about the acoustic identification of certain bat species in Switzerland, tape recordings of the acoustic behaviour of *Nyctalus leisleri* and *Pipistrellus savii* were made. Until now only little information on the echolocation sounds of both species had been available. Hooper (1969) described the approximate frequency range and pulse repetition rate of captive *N. leisleri*. Konstantinov and Makarov (1973), and Patljakevitsch (1980) studied echolocation pulses of captive *P. savii*. The present paper describes search calls of free flying individuals of both species as well as cries of *N. leisleri* which are assumed to be social calls.

Material and methods

Search pulses of free flying *N. leisleri* were recorded in the southern Alps (N = 38 analysed signals) and northern alps (N = 140) of Switzerland. One *N. leisleri*, marked with reflective tape on a ring, was recognized some weeks after release in the northern Alps. Search pulses were recorded, when this bat was hunting above a road with street lights. A further batch of signals (N = 26) of a single individual in the plane near Berne has been analysed. For statistical analysis all the recordings were pooled (N = 204 analysed signals).

Search pulses of free flying *P. savii* were recorded in northern (N = 73 analysed signals), central (N = 90) and southern (N = 73) parts of the Swiss Alps. For statistical analysis all the recordings were again pooled (N = 236 analysed signals).

"The distinction between search and approach calls is arbitrary as they are part of a continuum. . ." (Fenton and Bell 1981). For this study only pulses being part of more or less regular

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sequences were analysed. Pulses whose BW/T-factor (kHz/ms) exceeded a value of 1.0 were not considered as search pulses and excluded from calculations.

In addition to the above signal sample obtained from free flying bats, echolocation pulses of several individuals of *P. savii* and *N. leisleri* were collected, when the bats were released after net trapping. The aim was to get reference signals from known individuals in order to facilitate the acoustic recognition of free flying bats.

All ultrasounds were picked up with a modified QMC S100 ultrasound detector connected to a frequency divider, developped and built by K. Zbinden, University of Berne. The frequency divider produces a sinusoidal waveform at one eighth of the original frequency and retains the envelope of the original signal. Further specifications are: Frequency range 10–220 kHz (+/−2 dB), S/N-ratio 55 dB (lin. 10–220 kHz), switchable HP-filter (20 kHz, 24 dB/octave). The transformed ultrasounds were recorded with a SONY TC-D 5M on metal cassettes (−3 dB at 15 kHz).

The recordings were analysed on a Nicolet type 3091 dual channel digital oscilloscope (2×4K words) using a period meter (zero crossing detector, developped by D. Hartley, Queen Mary College, London and K. Zbinden, University of Berne, who also built the instrument). Of each pulse the following signal variables were measured: The start frequency (fs), the instantaneous frequency at maximum signal amplitude (fmax), the center frequency (fc) at half the pulse duration and the end frequency (fe). The frequency variables were estimated to an accuracy of +/−0.4 kHz in realtime. The sweep bandwidth was calculated as BW = fs-fe. The pulse durations were estimated to an accuracy of approx. 0.2 ms and intervals between pulses (from pulse center to pulse center) to an accuracy of +/ −2 ms.

Averaged power spectra were obtained on an FFT-analyser type 2033 of B & K, Denmark (400 lines, flat weighting, linear average mode, RMS spectrum).

Computations of quartiles and modes were made according to Sachs (1978). Preceeding the computations all the measurements were classified using class widths of 10 ms for interval durations, 1 ms for pulse durations and 0.8 kHz for frequencies (real time). Goodness-of-fit tests for normal distribution, correlation coefficients and arithmetic means were computed on a HP-71B calculator, using its AMPI stastistics library.

In those cases where the distribution did not conform to the standard probability models, the median instead of the arithmetic mean was taken as a representative measure of location (or of central tendency).

The interquartile-range $Q_{(0.75)}$–$Q_{(0.25)}$, which contains 50% of a sample, was used as a measure of dispersion. To allow a comparison with the data obtained by other authors, both the parametric and nonparametric statistics were calculated.

Results

Nyctalus leisleri

Intervals between search pulses showed a bimodal distribution and varied considerably (Fig. 1A). A first prominent mode was at 243 ms and a second weaker mode at 350 ms (both modes were estimated using the original class width of 10 ms).

The pulse durations were normally distributed (χ^2=9.5, df=10) with a median of 9.2 ms (Fig. 1B).

The distributions of the four frequency variables are shown in Figure 2, their statistical parameters in Table 1. A goodness-of-fit test was consistent with normal distribution in the case of the center frequency (χ^2=12.3, df=9), the maximum frequency (χ^2=12.2, df=8) and the end frequency (χ^2=2.8, df=7), but not the bandwidth (χ^2=351, df=8) and the start frequency (χ^2=71.3, df=14), which skewed towards the higher frequencies.

In this sample the end frequency had the smallest statistical dispersion. The averaged power spectrum of 50 search pulses showed a dominant frequency at 23.8 kHz and a −6 dB spectrum bandwidth of 2.9 kHz (Fig. 3).

Most search pulses of *N. leisleri* were frequency modulated by a small amount only. Nine of 204 pulses (T=3.7–12.2 ms) were of constant frequency (CF) in the range of 22.4–27.2 kHz. In the distribution of bandwidth (BW) the modal class and both classes on each side of it (range 0.8 to 2.4 kHz) contained 76% of the analysed pulses (see Fig. 1C). Pulses emitted during the approach phase however, frequently had a very steep frequency modulation and a bandwidth of more than 30 kHz.

Search pulses of *N. leisleri* often increased rapidly to a high amplitude level at their beginning (Fig. 4). When listening to the bats by means of a broadband detector this

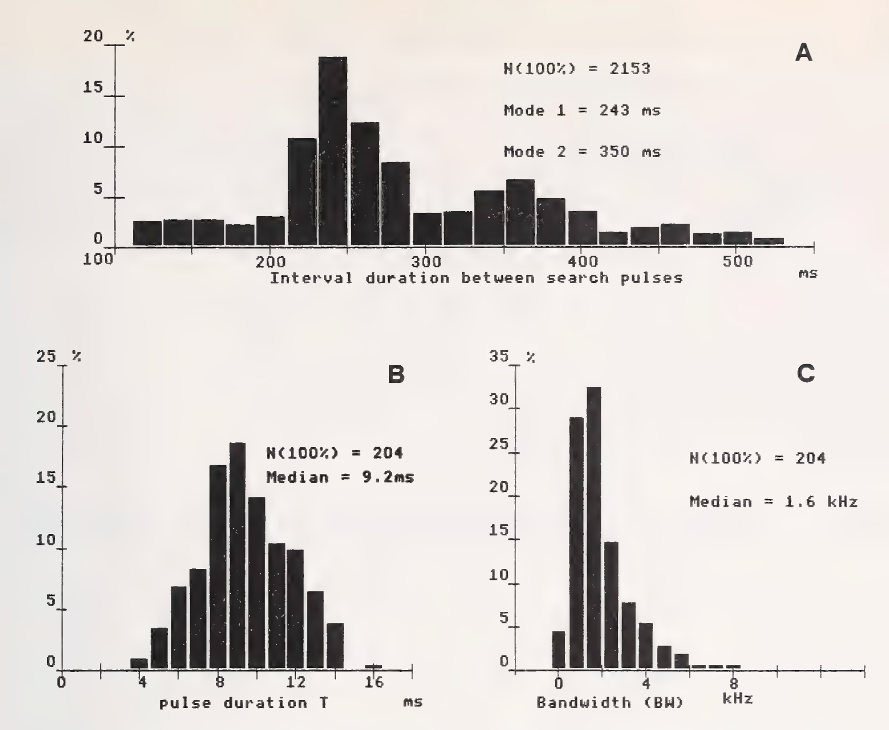


Fig. 1. Nyctalus leisleri. A: Interval duration between search pulses (from pulse center to pulse center). Width of classes is 20 ms. B: Duration of search pulses. Width of classes is 1 ms. C: Sweep bandwidth (BW) of search pulses. Width of classes is 0.8 kHz

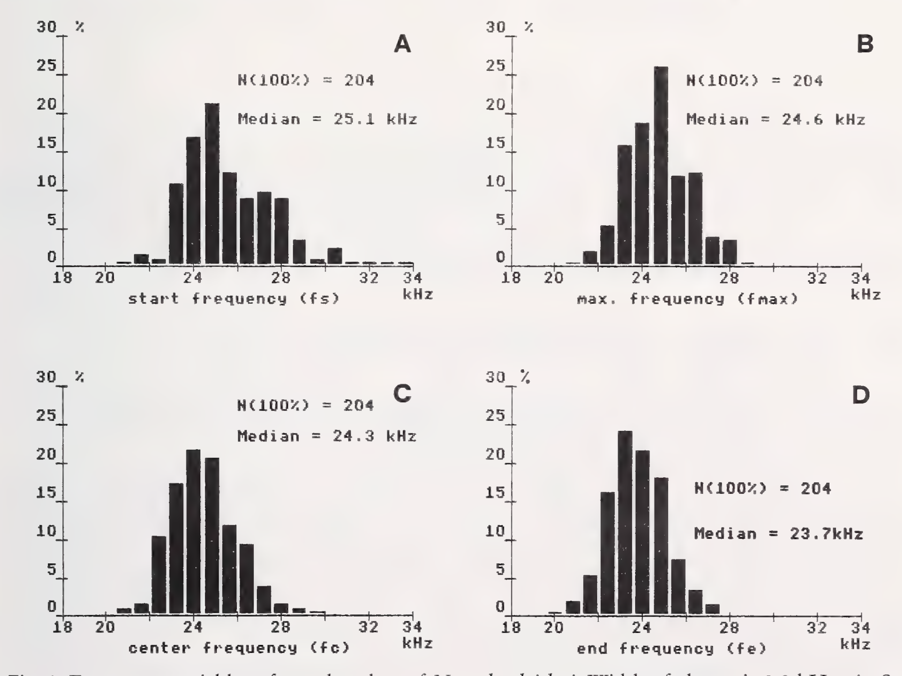


Fig. 2. Frequency variables of search pulses of *Nyctalus leisleri.* Width of classes is 0.8 kHz. A: Start frequency at the beginning of a pulse. B: Instantaneous frequency at maximum signal amplitude. C: Center frequency at half the pulse duration. D: End frequency

Table 1. **Parameter values of search pulses (N = 204) of *Nyctalus leisleri*, as shown in Figs. 1 and 2**

	Q1	Median	Q3	Q3–Q1	95 % confidence interval of $\bar{x}$
Pulse duration T (ms)	7.8	9.2	11.1	3.3	9.1– 9.7
Start frequency fs (kHz)	24.1	25.1	27.0	2.9	25.3–25.9
Maximum frequency fmax (kHz)	23.7	24.6	25.7	2.0	24.5–24.9
Center frequency fc (kHz)	23.4	24.3	25.4	2.0	24.2–24.7
End frequency fe (kHz)	22.8	23.7	24.6	1.8	23.5–23.9
Bandwidth BW (kHz)	1.0	1.6	2.5	1.5	–

Q1 and Q3 are the quartiles $Q_{<0.25>}$ and $Q_{<0.75>}$ of the distributions. Q3–Q1 is the interval that contains 50 % of the whole sample (or 50 % of the frequency distribution area).

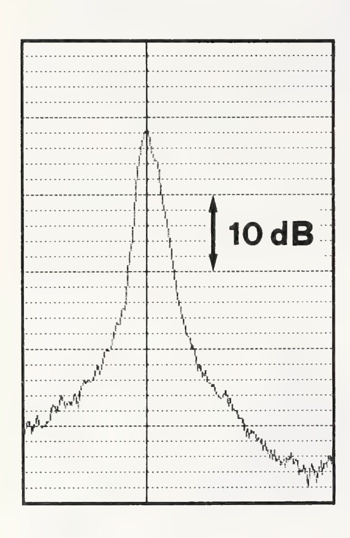


Fig. 3. Nyctalus leisleri. Averaged power spectrum of 50 search pulses (400 lines, RMS-spectrum type, flat weighting, linear averaging). Frequency span: 8–48 kHz. The vertical cursor is at the dominant frequency of 23.8 kHz. The −6 dB spectrum bandwidth is 2.9 kHz

resulted in an explosive sound, a phenomenon not found to the same extent in other bat species of Switzerland.

Due to the recording system used, the presence of harmonics could not be checked systematically. In a few search pulses 'steps' in the period plot seemed to indicate the eventual presence of a strong second harmonic, however.

It is known that there may exist relationships e.g. between pulse duration and bandwidth, depending on the function of a pulse (Tupinier et al. 1980; Hartley 1985). Correlation coefficients were computed (Tab. 2) to check interesting relations between the measured variables of search pulses. Negative correlations between pulse duration T and the four frequency variables were found. This indicates that shorter search pulses tended to have higher values in all the frequency variables. There was no significant correlation between bandwidth and search pulse duration. This and the positive correlation between the end and the start frequency means that short pulses as a whole were situated higher in the frequency scale.

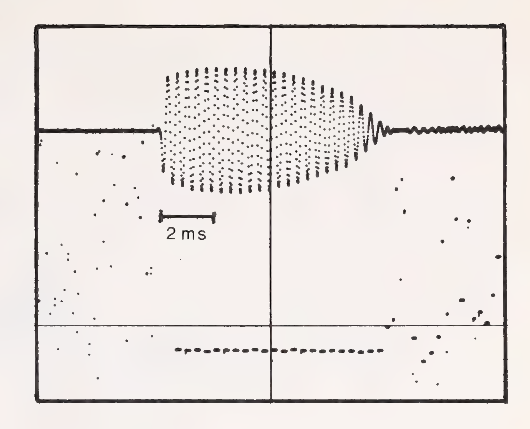


Fig. 4. Characteristic search pulse of *Nyctalus leisleri.* Oscillogram with superimposed frequency plot. T=8.2 ms, fs=23.2 kHz, fmax=22.4 kHz, fc=22.4 kHz, fe=22.4 kHz. The vertical cursor indicates the pulse center (half duration). The horizontal cursor is at 30 kHz in the frequency plot

Table 2. **Correlation coefficients (arranged from highest to lowest) of selected variables of a random subsample of 49 search pulses of *Nyctalus leisleri***

r(fe, fs) = +0.777	r(fc, T) = −0.653	r(BW, T) = +0.001
r(fe, T) = −0.739	r(fs, T) = −0.554	
r(fmax, T) = −0.667	r(BW, fe) = +0.037	

A goodness-of-fit test was consistent with normal distribution for all the variables. T: χ^2=8.8 (df=8). fs: χ^2=2.5 (df=5). fmax: χ^2=2.4 (df=6). fc: χ^2=3.8 (df=4). fe: χ^2=3.8 (df=5). BW: χ^2 =7.4 (df=3). The null hypothesis, Ho: p=0, can be rejected at $P<0.001$, for all the r-values, except r (BW, fe) and r (BW, T), where $P>0.1$

Social calls of *N. leisleri*

On 4 July 1986 at 2:30 MEZ, two *N. leisleri* were hunting insects above the street lights at Meiringen (Northern Alps). In addition to echolocation signals, complex patterns of cries, probably of social function, were recorded. It is not known whether the calls were emitted by both animals. Two types of social calls will subsequently be described.

The first type of social call consisted of a group of four pulses (Fig. 5). Four of these calls were emitted in short sequence separated by intervals of 195–485 ms, containing a number of echolocation pulses.

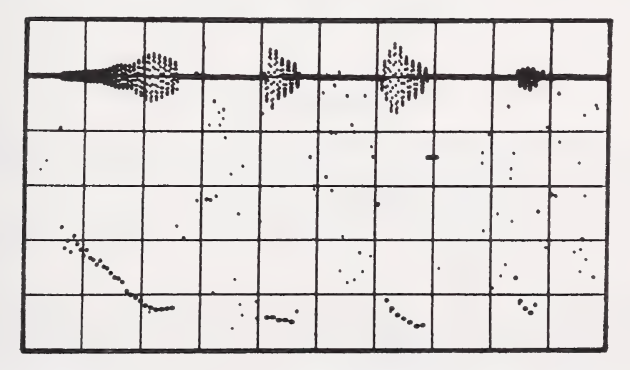


Fig. 5. Nyctalus leisleri. Social call type 1. Oscillogram with superimposed frequency plots (horizontal axis 4.0 ms/div). Cf. text for further details

With about 9 ms the first cry of a group had the longest duration. It used to start at 38 kHz with a short, shallow frequency modulation, followed by a long, steeper part and ended at 22 kHz with shallow modulation again. In one group the change in the modulation rate of the first pulse occurred abruptly and resulted in an "elbow"-shaped frequency plot (Fig. 5).

The following three pulses in the groups were all different from the first one. Their pulse duration was shorter and varied from 1.6 to 4.8 ms. In each group the last pulse was the shortest. The second, third and fourth pulse started at 20–27 kHz with a maximum amplitude at approx. 21 kHz and ended at 16–20 kHz. They, and especially the fourth pulse in each group, appeared to include higher harmonics of varying strength. The intervals between pulses were in the range of 4.7–11.5 ms.

In late August 1986 similar social calls were recorded in southern Switzerland. They were emitted by two or three unknown bats which stayed in a group of chestnuttrees (*Castanea sativa*). The calls consisted of three to five pulses. The first pulses had a duration of 9–14 ms. They started with shallow frequency modulation at 25–28 kHz. The modulation rate became steeper in the second half of the pulse which ended at a frequency of 18–20 kHz. The plot of the instantaneous frequency showed a convex curve. The following pulses in a group always had a shorter duration (1–5 ms). Their lowest frequency varied from 14 to 21 kHz.

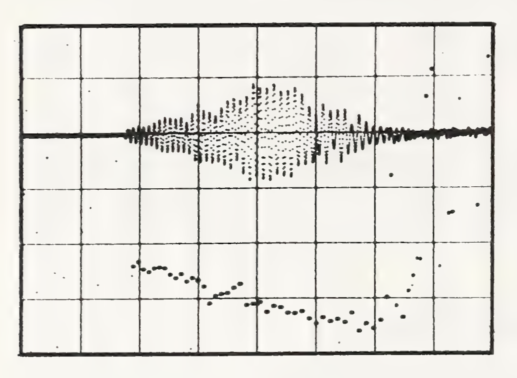


Fig. 6. Nyctalus leisleri. Social call type 2. Oscillogram with superimposed frequency plot (horizontal axis 5.4 ms/div.). T=24 ms, fs=17 kHz, fmax=fc=13 kHz, fe=10 kHz

At Meiringen a second type of social call of *N. leisleri* was recorded three times, when a pipistrelle bat (*P. pipistrellus*) passed (Fig. 6). The pulse duration varied from 24 to 27 ms. All pulses were more or less linear period modulated, started at 18–17 kHz and ended at 11–10 kHz. The FFT power spectrum of the pulse shown in Figure 6 had a peak at 12.6 kHz and a −6 dB spectrum bandwidth of 1.4 kHz.

The same type of social call was recorded in southern Switzerland from the same two or three unidentified bats as described above.

Mean values +/− standard deviation of 22 analysed signals from southern Switzerland were: T=22.1 +/−2.17 ms, fs=19.2 +/−0.78 kHz, fmax=12.5 +/−0.57 kHz, fc=13.7 +/ −0.57 kHz, fe=11.2 +/−0.39 kHz and BW=8.0 +/−0.63 kHz. These parameter values are close to those of the calls recorded in northern Switzerland.

Pipistrellus savii

The distribution of intervals between search pulses (Fig. 7A) was again multimodal and had a prominent peak at about 190 ms. There was a second much smaller mode at 294 ms (both modes were computed using the original class width of 10 ms).

For all the variables T, fs, fmax, fc, fe and BW the hypothesis of normal distribution could not be maintained (Chi-square goodness-of-fit test). Thus the median and the quartiles are better suited to characterize the distributions.

In the distribution of pulse durations (median: 12.1 ms) 50% of the sample were between 10.9 ms ($Q_{0.25}$) and 13.8 ms ($Q_{0.75}$) (Fig. 7B and Tab. 3). Two pulses in the sample were considerably longer (20 and 21 ms).

Although their BW/T is not higher than 1.0, five pulses of the sample may be classified

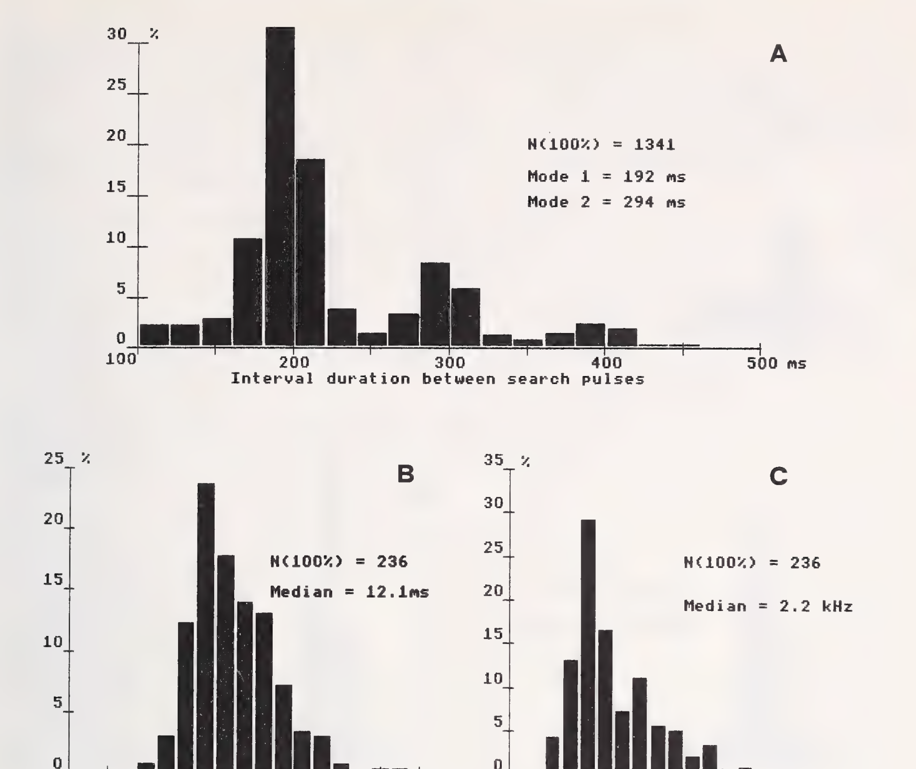


Fig. 7. Pipistrellus savii. A: Interval duration between search pulses (from pulse center to pulse center). Width of classes is 20 ms. B: Duration of search pulses. Width of classes is 1 ms. C: Sweep bandwidth (BW) of search pulses. Width of classes is 0.8 kHz

as approach pulses when their high start frequencies and bandwidths are considered (Figs. 8A and 7C). Parameter estimation excluding these five outliers does not shift the obtained results substantially, however.

The end frequency had a very prominent peak at 32 kHz and the smallest dispersion (Fig. 8D). The center frequency (Fig. 8C) and the maximum frequency (Fig. 8B) also had a rather small dispersion. Again the distribution of the start frequency (Fig. 8A) was platycurtic, skewed towards higher frequencies and was most dispersed. The averaged power spectrum of 50 search pulses had a dominant frequency of 33.2 kHz and a −6 dB spectrum bandwidth of 1.6 kHz (Fig. 9).

The bandwidth of the search pulses (Fig. 7C) varied more than in *Nyctalus leisleri* but, with 1.6 kHz, had the same peak value. The modal class and both classes on each side of it (range 0.8 to 2.4 kHz) contained only about 59% of the sample.

Nine search pulses (T=11–18 ms) of the whole sample were of constant frequency, in the range of 32.0–33.6 kHz.

Table 4 shows the correlation coefficients of selected variables of a random subsample of 49 search pulses of *P. savii.*

The three strongest correlations indicate that shorter search pulses tended to have a higher start frequency and a larger sweep bandwidth.

A
N(100%) = 236
Median = 34.2 kHz
40 % 35 30 25 20 15 10 5 0
30 34 38 42 46 kHz
start frequency (fs)

B
N(100%) = 236
Median = 33.2 kHz
40 % 35 30 25 20 15 10 5 0
28 32 36 40 44 kHz
max. frequency (fmax)

C
N(100%) = 236
Median = 32.8 kHz
40 % 35 30 25 20 15 10 5 0
28 32 36 40 44 kHz
center frequency (fc)

D
N(100%) = 236
Median = 32.0 kHz
40 % 35 30 25 20 15 10 5 0
28 32 36 40 44 kHz
end frequency (fe)

Fig. 8. Frequency variables of search pulses of *Pipistrellus savii.* Width of classes is 0.8 kHz. A: Start frequency at the beginning of a pulse. B: Instantaneous frequency at maximum signal amplitude. C: Center frequency at half the pulse duration. D: End frequency

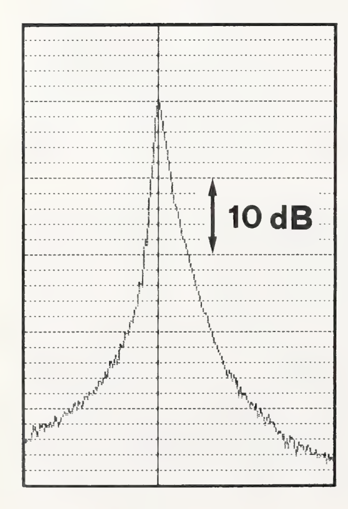


Fig. 9. Pipistrellus savii. Averaged power spectrum of 50 search pulses (settings cf. Fig. 3). Frequency span: 16–56 kHz. The vertical cursor is at the dominant frequency: 33.2 kHz. The −6 dB spectrum bandwidth is 1.6 kHz

Fig. 10. Characteristic search pulse of *Pipistrellus savii.* Oscillogram with superimposed frequency plot. T=10.9 ms, fs=33.6 kHz, fmax=32.8 kHz, fc=32.8 kHz, fe=32.0 kHz. The vertical cursor indicates the pulse center. The horizontal cursor is at 30 kHz in the frequency plot

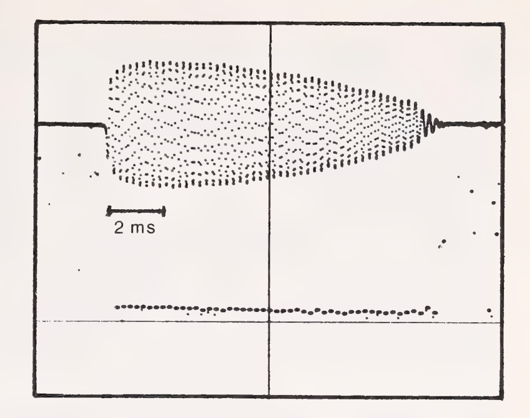


Table 3. **Parameter values of search pulses (N=236) of *Pipistrellus savii,* as shown in Figs. 7 and 8**

	Q1	Median	Q3	Q3–Q1	95 % confidence interval of $\bar{x}$
Pulse duration T (ms)	10.9	12.1	13.8	2.9	12.1–12.7
Start frequency fs (kHz)	33.1	34.2	36.0	2.9	34.4–35.0
Maximum frequency fmax (kHz)	32.5	33.2	33.7	1.2	33.1–33.4
Center frequency fc (kHz)	32.2	32.8	33.4	1.2	32.6–32.9
End frequency fe (kHz)	31.4	32.0	32.5	1.1	31.8–32.0
Bandwidth BW (kHz)	1.4	2.2	3.9	2.5	–

Q1 and Q3 are the quartiles $Q_{\langle 0.25 \rangle}$ and $Q_{\langle 0.75 \rangle}$ of the distributions. Q3–Q1 is the interval that contains 50 % of the whole sample (or 50 % of the frequency distribution area)

Table 4. **Correlation coefficients (arranged from highest to lowest) of a selected variables of a random subsample of 49 search pulses of *Pipistrellus savii***

r(fs, T) = −0.607***	r(fmax, T) = −0.411**	r(BW, fe) = +0.047
r(BW, T) = −0.514***	r(fc, T) = −0.357*	
r(fe, fs) = +0.451**	r(fe, T) = −.300*	

A goodness-of-fit test was consistent with normal distribution for all the variables. T: χ^2=4.8 (df =8). fs: χ^2=3.9 (df=6). fmax: χ^2=5.3 (df=6). fc: χ^2=1.3 (df=4). fe: χ^2=2.3 (df=3). BW: χ^2=11.2 (df=6). Significance levels to reject the null hypothesis, Ho: p=0, are: ***P<0.001, **P<0.01 and &P<0.05. But P>0.1 für r(BW, fe)

Discussion

During the field work I realized that bats did show a different acoustic behaviour, depending on how they were released. If they were allowed to decide themselves when to fly away from the hand of the observer, most bats emitted short FM pulses with a steep frequency modulation.

But when the bats were thrown upwards in the air, there was a good chance that they changed from the initial steep FM pulses to shallow modulated search pulses still within the range of the recording microphone.

Generally pipistrelle bats (*P. pipistrellus, P. nathusii, P. kuhli* and *P. savii*) used to change quickly from approach pulses to search pulses and to turn round close to the place where they had been released. Sometimes they even started to hunt insects in the proximity of the observer.

Noctule bats (*N. noctula* and *N. leisleri*) on the other hand often used to fly straight away from the observer in fast flight and it was difficult to record search calls in this way. For this reason tape recordings of released and in their behaviour probably disturbed bats were not taken into account for the analysis so far.

To allow a comparison, parameter values of a pooled sample of 44 pulses recorded from 12 *N. leisleri* when they were thrown in the air, is shown in Table 5.

Table 5. **Parameter values of echolocation pulses (N=44) of 12 *Nyctalus leisleri*, recorded shortly after the bats had been released**

	Q1	Median	Q3	Q3–Q1	Minimum value	Maximum value
Pulse duration T (ms)	9.8	11.7	12.4	2.6	7.2	15.9
Start frequency fs (kHz)	25.0	27.0	32.1	7.1	21.6	48.8
Maximum frequency fmax (kHz)	23.9	24.8	26.8	2.9	21.6	31.2
Center frequency fc (kHz)	23.7	24.6	26.2	2.5	21.6	30.4
End frequency fe (kHz)	23.0	23.9	25.1	2.1	20.8	27.2
Bandwidth BW (kHz)	1.5	3.3	7.3	5.8	0	21.6

Q1 and Q3 are the quartiles $Q_{(0.25)}$ and $Q_{(0.75)}$ of the distributions. Q3–Q1 contains 50 % of the whole sample (or 50 % of the frequency distribution area)

The parameter values of the pulse sample of released bats were generally similar to the parameter values of the search pulses of undisturbed, free flying *N. leisleri* (compare with Tab. 1). The end frequency and the center frequency showed the least divergence.

The extreme upper values of the start frequency and the bandwidth in Table 5 indicate that the sample contained a few pulses similar to those emitted in the approach phase.

In general terms the variables of search pulses analysed in this study varied less in *P. savii* than in *N. leisleri*. This points to a more regular flight behaviour in *P. savii*. I could not see Savi's pipistrelles when they were hunting along the streets, since they used to fly higher than the bright streetlights at approximately 10 m above ground.

The flight height of the Lesser noctules varied considerably. On average the bats were hunting at the level of the street lights, but I observed Lesser noctules pursuing moths down to the ground or searching much higher than the street lights. This flexible flight behaviour may be the reason for the large dispersion of pulse interval durations.

Search calls of *P. savii* had the lowest end- and center frequency of the four *Pipistrellus* species (*P. pipistrellus. P. nathusii, P. kuhli, P. savii*) that occur in Switzerland (unpubl. data). The search calls of Savi's pipistrelle appear to be closer to those of *Eptesicus nilssoni* than to those of the other three *Pipistrellus* species. This similarity between *E. nilssoni* and *P. savii* can be affirmed by their resembling appearance (e.g. colour of the skin, shape of

the ear, projecting tail-tip), a fact already mentioned by MILLER (1912, p. 224). HORACEK and HANAK (1986) now propose to place *P. savii* in a separate genus *Hypsugo*.

The correlations showed that in *N. leisleri* shorter pulses were generally of higher frequency, but without an increase of the bandwidth of the fundamental harmonic. It is conceivable that in fact a higher sweep bandwidth was realized by introducing additional harmonics, which of course were not detectable by the system used in this study. In general terms the values of the correlation coefficients are smaller in *P. savii* than in *N. leisleri*. The relations between bandwidth BW and pulse duration T were markedly different in the two species. In *N. leisleri* there was no significant correlation between these two variables in the case of search pulses. In *P. savii* on the other hand a significant negative correlation existed between the bandwidth and the pulse duration: When the search pulse duration decreased, their bandwidth increased. Since the end frequency showed only little variability, the higher bandwidth of short pulses was due to an increased start frequency. This is affirmed by its negative correlation to the pulse duration.

HOOPER (1969) and WATSON (1970) evaluated the frequency range of *N. leisleri* by means of a heterodyning detector (Holgate Ultrasonic Receiver) only. HOOPER (1969) determined 80 and 25 kHz as "upper and lower limits of the detected range of frequency sweep" and measured a pulse repetition rate of 8–10 pulses per sec (i.e. 125–100 ms interval duration) under indoor conditions (crawling). Only the lower frequency limit resembles the end frequencies of search calls presented in this paper.

WATSON (1970) gave an "approximate frequency range for field work" of 15–70 kHz, which should be valid for both noctule species (*N. noctula* and *N. leisleri*). This frequency range is far wider than the range of search calls of *N. leisleri* (20–34 kHz) reported here.

KONSTANTINOV and MAKAROV (1973) analysed 44 signals of one *P. savii*. The short pulse durations (0.8–2.3 ms) as well as the high start frequencies (90–100 kHz) and end frequencies (40–45 kHz) are consistent with indoor conditions. The authors mentioned a second harmonic and a near linear frequency modulation in the first part of the signal.

PATLJAKEVITSCH (1980) measured a mean start frequency of 71.3 kHz and a mean end frequency of 35.7 kHz from handheld *P. savii*. This is still above the highest end frequency I have found in search pulses. The pulse duration of his handheld bats ranged between 0.4 and 36 ms. When the bats were flying away from the wall of an aviary he measured pulse durations up to 5 ms. In our recordings the pulse durations were in the range of 8 to 21 ms.

The evidence of constant frequency (CF) pulses in *N. leisleri* and *P. savii* is not surprising. Pure CF-pulses have formerly been reported of *N. noctula* (PYE 1978, 1980; VOGLER and NEUWEILER 1983) and *P. pipistrellus* (PYE 1978, 1980; AHLEN 1981; MILLER and DEGN 1981).

A sequential alternation of the end frequency on a pulse to pulse basis, as known from *N. noctula* (AHLEN 1981; MILLER and DEGN 1981; HARTLEY 1985), was rarely observed in *N. leisleri*. On the contrary, pulse sequences with end frequencies varying less than 1 kHz seem to be characteristic for this species.

It is interesting to compare the positions of the modes of intervals between search pulses. In *P. savii* I got the equation 'mode 2 = 1.53 × mode 1' and in *N. leisleri* 'mode 2 = 1.44 × mode 1'. A comparable relation between modes can be established from the interval distribution of search pulses of *Nyctalus noctula* (high flight) in AHLEN (1981).

For *N. noctula* HARTLEY (1985) measured a wing beat rate of 9/sec (= 111 ms interval duration) in pursuit flight, corresponding to one pulse per wing beat. In cruising flight he found two wing beats per pulse. The interpulse intervals (cruising flight) presented in this paper might be consistent with the hypothesis of two wing beats per pulse (first mode) and three wing beats per pulse (second mode).

Due to lacking behavioural data, the social calls described in this paper should be interpreted with caution. The first type of social call, recorded in July 1986 at Meiringen, appeared to be an interaction between two individuals of *N. leisleri*. The first and the

second type of social calls were also recorded when a *P. pipistrellus* passed the Lesser noctules. At the same time sequences of short pulses (3–4 ms, probably multiharmonic) with end frequencies of about 10 kHz (interpulse duration ca. 6 ms) were recorded. Figure 11 shows part of such a sequence enclosing an echolocation pulse.

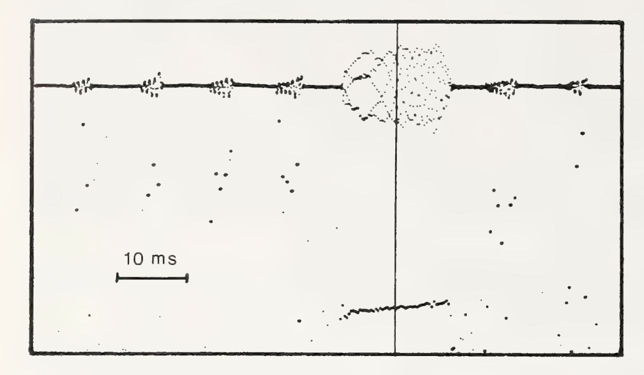


Fig. 11. Nyctalus leisleri. Oscillogram and superimposed period plot showing a search pulse (T=14.9 ms, fs=28.0 kHz, fc=24.8 kHz, fmax=fe=24.0 kHz) and part of a sequence of ten short pulses of social context (T= 2.7–4.2 ms, fe= ca. 10 kHz, interpulse duration = 4.6–8 ms). The vertical cursor indicates the pulse center of the search pulse. The total time from the start of the first short pulse to the end of the tenth short pulse was 113 ms

In southern Switzerland the social calls resembling type 1 and 2 of Meiringen were recorded during the mating season (August 86) and there was no indication that interactions with other species occurred. On the basis of the similar structure and the combined occurrence of call type 1 and 2 at Meiringen as well as in Southern Switzerland, I assume that these two types of social calls were actually emitted by individuals of *Nyctalus leisleri* at both recording sites.

In the field, the social call of type 2 could be confused with echolocation pulses of *Tadarida teniotis* (Zbinden and Zingg 1986). But signal analysis shows that search calls of *T. teniotis* have not such a high start frequency and are not normally of linear period modulation.

Acknowledgements

I wish to thank Elisabeth Bucher and Raphaël Arlettaz for their precious help in the fieldwork. Prof. V. Aellen kindly supplied me with Russian literature, parts of which were translated by Mrs. V. Schnell and R. Hodel. I thank Dr. O. Bernath, Departement of Audiology of the Berne University Hospital, for permitting the use of the FFT-analyser. I am greatly indebted to Dr. Karl Zbinden for critically reading the manuscript, making important suggestions for its improvement and correcting the text. This study was supported by the Swiss National Science Foundation (grant no. 3.177-0.85).

Zusammenfassung

Suchflugortungslaute von Nyctalus leisleri und Pipistrellus savii (Mammalia: Chiroptera) in der Schweiz

Suchflugortungslaute jagender *Nyctalus leisleri* und *Pipistrellus savii* wurden mittels QMC S100 Detektor und 8:1 Frequenzteiler auf der schweizerischen Alpennord- und Alpensüdseite registriert. Bei beiden Arten wurden sowohl schwach frequenzmodulierte als auch konstantfrequente Suchfluglaute festgestellt.

Für 204 analysierte Suchfluglaute von *N. leisleri* waren folgende Medianwerte charakteristisch: Signaldauer 9.2 ms, Anfangsfrequenz 25.1 kHz, Zentrumsfrequenz 24.3 kHz, Endfrequenz 23.7 kHz, Signal-Bandbreite 1.6 kHz. Die Intervalldauer (N=2153) zwischen den Signalen zeigte eine bimodale Verteilung, mit einem starken Modus bei 243 ms und einem zweiten, schwächeren bei 350 ms.

Für 236 Suchfluglaute von *P. savii* waren folgende Medianwerte typisch: Signaldauer 12.1 ms, Anfangsfrequenz 34.2 kHz, Zentrumsfrequenz 32.8 kHz, Endfrequenz 32.0 kHz, Signal-Bandbreite 2.2 kHz. Die Intervalldauer (N=1341) zwischen den Signalen war bimodal verteilt, mit einem starken Modus bei 192 ms und einem zweiten, schwächeren bei 294 ms. Bei beiden Spezies wurden zwischen verschiedenen Variablen der Suchfluglaute signifikante Korrelationen ermittelt.

Zusätzlich werden als Soziallaute interpretierte Ruftypen von *N. leisleri* beschrieben. Der erste Typ bestand aus einer Gruppe von vier Lauten im Frequenzbereich von 38–16 kHz. Der zweite Typ, ein linear periodenmodulierter Einzellaut (T=20–27 ms), überstreicht ein Frequenzband von 21–10 kHz und kann im Felde mit Ortungsrufen von *Tadarida teniotis* verwechselt werden.

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Z. Säugetierkunde 53 (1988) 294–300

ISSN 0044-3468

The development of visual acuity in treeshrews *(Tupaia belangeri)*

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Receipt of Ms. 1. 6. 1987

Abstract

Ontogenetic development of visual acuity was tested in 14 young treeshrews *(Tupaia belangeri)* from the moment of eye opening (day 16 to 23) until leaving their nest (day 30 to 34), using an optomotoric drum. First optokinetic nystagmus (OKN) was found between day 4 and 5 after eye opening with individual values of visual acuity varying considerably between 34,5 and 370 minutes of arc. Before leaving the nest all values were about 11 minutes. In general, the longer the process of eye opening took (from a few hours to three days) the later was the first OKN. No correlation was found between the onset of eye opening and the first OKN. There were no differences in the development of visual acuity between the two sexes. In addition to the optomotoric drum training, visual acuity of two adult male tupaias was determined using a visual discrimination choice apparatus. According to all tests, visual acuity of adult treeshrews was found to be 10 and 8,6 minutes respectively. The extent of visual acuity found in this study was compared with that of some primates.

Introduction

Currently the Tupaiidae are considered to be the group of recent mammals that is most similar to the ancestors of primates (STARCK 1978). However, despite numerous morphological, physiological and ethological investigations, there has been no final decision as to their relationship to other mammalian taxa (LUCKETT 1980). Therefore, they have been placed in a separate mammalian order, Scandentia. The diurnal and semiarboreal tupaias live in southeast Asia, where males occupy overlapping home ranges with females (KAWAMICHI and KAWAMICHI 1979). They feed on different sorts of fruit, insects and even some smaller vertebrates. Their senses of smell and hearing as well as their vision are highly developed.

Visual acuity of adult tupaias has already been determined with visual discrimination training but with different results. Thus, ORDY and SAMORAJSKI (1968) have found a visual angle of 0,5 to 1,5 min of arc and SCHÄFER (1969) has reported one of 6,8 min of arc. Even though research on the visual acuity of the eye in various groups of animals has been reported in the past and with many different methods (RAHMANN 1967; BOOTHE et al. 1985; for review), so far there is no information on the ontogenetic development of vision in *Tupaia belangeri*.

The purpose of this study is to show how visual acuity develops in young tupaias from the moment of eye opening until after they leave their nests, and thus, to provide a basis for comparison with the visual development of various primates.

Material and methods

Determination of visual acuity during development of tupaias by means of the optomotoric nystagmus (OKN)

14 young tupaias born at the breeding colony at the Department of Zoology, University of Stuttgart Hohenheim, were tested. Housing and maintenance of breeding pairs and postnatal behavioral development of young has been described previously (HERTENSTEIN et al. 1987). Tupaias are born

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blind. Data collection began at eye opening about 19 days after birth, and continued another 10 to 12 days until they had left their nest box for the first time. At this time tupaias develop a highly coordinated locomotor ability to move through their semi-arboreal environment and react promptly to potential dangers.

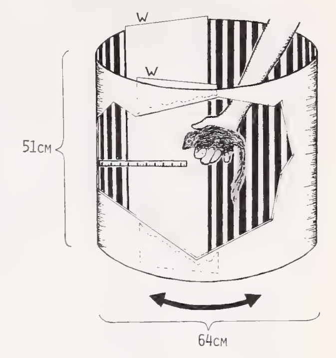


Fig. 1. Optomotoric drum for determination of visual acuity of young treeshrews. (w = white sheet, used to reduce the visual field of the animal)

The experiments were conducted in an optomotoric drum having a height of 51 cm and a diameter of 64 cm, with vertical black and white stripes of equal width (Fig. 1). There were 15 different stripe-patterns each of them having a particular width of stripes ranging from 12 mm to 0,4 mm. A 75W bulb, hanging over the centre of the barrel, provided equal illumination. There were no windows or other light in the room. The animals were found to remain calm if held by hand while being tested. Visual acuity was tested once each day in the morning. The young were taken out of the parental cage within their nestboxes. The animals were allowed to adapt to the light for 15 to 20 min. Testing started with the pattern with the widest stripes (d = 12 mm) in a short distance (E = 10 cm, see Fig. 2). The distance E was increased, if the animal showed a clear optomotoric nystagmus (OKN). The next smaller stripe pattern was used once the distance between head and pattern could not be increased any further (diameter of the barrel = 32 cm). Visual acuity was calculated from the exact field of sight (E) at which, for a definite width of stripes (d), the animals still responded with an OKN, using the formula in Fig. 2.

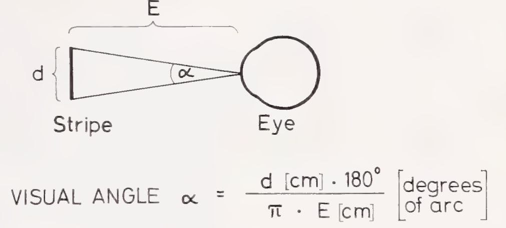


Fig. 2. Formula for calculating visual acuity. (See text for details)

As the attention of the animals decreased rapidly, they tried to leave the hand or simply went to sleep. Therefore many rests were necessary during each experiment and in some cases the test had to be broken off completely.

Determination of visual acuity in adult tupaias by means of visual discrimination tests

The tests in this case were run with two adult male tupaias of an age of 4½ and 7½ months respectively, both of which had been reared by hand (Hertenstein et al. 1987). The animals were kept individually in wooden cages of a size of 0,5 m^3, and containing branches for climbing, shelves for sitting upon and a sleeping box. The ground was covered by fine sawdust and straw. Their food consisted of tupaia-pellets (by Altromin) and water ad lib., in addition to fruit, sunflower seeds, nuts, oatmeal, egg and cat food given in rotation. Insects were not used in the diet, since mealworms *(Tenebrio larva)* were used as rewards in the discrimination tests.

The "two alternative discrimination apparatus" utilized was similar to training systems used to test visual acuity in golden hamsters *(Mesocricetus auratus)*, lemmings *(Lemmus lemmus, Myopus schisticolor)* and various species of american deermice *(Peromyscus)* (Rahmann 1961; Rahmann and Esser 1965; Rahmann and Rahmann 1966; Rahmann et al. 1968). From a start box (Fig. 3) the animals enter the choice box where they have to decide between one of two patterned doors at the end of the choice box, separated by a partition. The patterns for the discrimination experiments were fixed to the doors. The patterns could be changed quickly from one side to the other by pulling strings. If the animal chose the correct door, he received a peace of mealworm as a reward. The animals made their

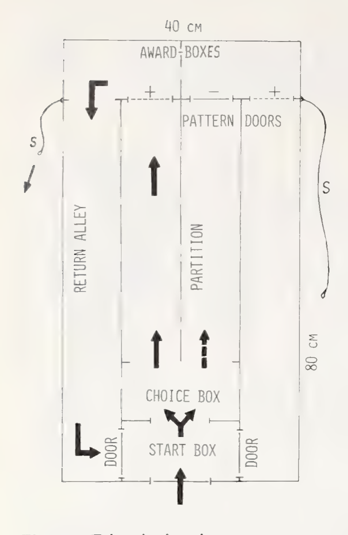


Fig. 3. Discrimination apparatus for determination of visual acuity of adult treeshrews. Pattern doors were manually alternated from left to right by pulling strings (s)

way back to the start box through return alleys, and the next test was started immediately. The whole apparatus was covered by a lid of plexiglas with slots for ventilation and presentation of rewards. A 75W bulb was hung just above the apparatus to illuminate the area around the patterned doors.

The tests were run once a day in the morning. The animals had to decide between a pattern of black and white vertical stripes of equal width (positive pattern, with reward) and a grey surface of the same brightness (negative pattern, door locked). The pattern was offered both on the right and on the left door, 20 times each, in a predeterminal, irregular order. There were 14 different patterns with various widths of stripes from 12 mm to 0,6 mm. The distance between the choice box and the pattern doors was 48 cm. The criterion of significance for the number of correct choices in 40 runs was fixed at 70%, for a 99% probability (KOLLER 1969). If the results of a test were not significant after an obvious lack of concentration of the test animal, the test was repeated with the same width of stripes on the following day. Quite often the result was then significant. To avoid the possibility that the animals were choosing different degrees of brightness of the patterns rather than deciding between stripe pattern and plain grey, a second series of tests was run, in which a choice had to be made between a vertical stripe pattern (positive pattern) and a horizontal one. All the other conditions of the test remained the same. Subsequently visual acuity was determined for a shorter choice distance of 27 cm, in order to have a comparison between greater and shorter choice distances.

♂ NO.	AGE AT EYE OPENING (DAYS)	FIRST OKN (DAYS AFTER EYE OPENING)	DURATION OF EYE OPENING (DAYS)
11	21	1	1
10	19	2	1
12	18	1	1
1	21	2	2
8	19	2	2
5	21	3	1
2	21	3	1
4	22	4	3
7	21	5	2

♀ NO.	AGE AT EYE OPENING (DAYS)	FIRST OKN (DAYS AFTER EYE OPENING)	DURATION OF EYE OPENING (DAYS)
13	20	1	1
14	19	1	1
7	21	3	2
3	21	3	3
9	19	4	2

Fig. 4. Development of visual acuity in 9 male and 5 female treeshrews. (For youngsters from the same litter identical symbols are used)

Results

Development of visual acuity during development of *Tupaia belangeri*

As shown in fig. 4a and b, four animals responded with a clear optomotoric reaction on the first day after eye opening. A first reaction was shown by three animals on the second day after eye opening, three on the third day, two on the fourth and one on the fifth. Within this period the individual visual angle varied considerably (34,5 min to 370 min = 6,2°). During the following eight days the range of the values decreased and, by the time the animals left their nests, they had reached a similar level of 11±0.75 minutes in the males and of 11,7±2,68 minutes in the females. The great interindividual differences in the first occurence of an OKN and the values for visual acuity might be caused not only by different visual efficiency, but also by the stress on particularly sensitive animals when being handled.

When their eyes started to open the test animals were between 18 and 22 days old. Separation of the eyelids took as long as three days but, in other cases, just a few hours. Notwithstanding how long the process of the eye opening took, the start of the process was counted as day number one. The first optomotoric response tended to be delayed when the process of eye opening took longer (see tables in Fig. 4a and b). No correlation between the age of the test animals at the start of the eye opening and the first OKN was found.

Visual acuity of adult tupaias

First, the animals were allowed to become familiar with the discrimination choice apparatus. They were rewarded if they used the striped door by chance (width of stripes in this case 12 mm). On the second test day test animal H (VT_H) already chose the striped door significantly more often than the plain grey door. Test animal W (VT_W), which was only 4½ months old, seemed nervous during the daily 5 to 10 minutes in the apparatus and took 7 days before he chose significantly between the two alternatives. To determine visual acuity (minimum separabile = perception of separation between stripes), the width of stripes was gradually reduced, from 7 to 0,6 mm, during the following days of testing, whereas the length of the partition was 48 cm. The door with the negative pattern remained locked. An attempt to go down the wrong alley for more than one head-length was scored at a miss. VT_H chose significantly between stripes and plain grey down to a width of stripes of 1,4 mm (see Fig. 5). This is equivalent to a visual angle of 10 minutes of arc. VT_W discriminated a stripe width of 12 mm, equivalent to a visual angle of 8,6 minutes of arc. Visual acuity for choosing between horizontal and vertical stripes was 11,5 minutes for VT_H and 10 for VT_W. This is virtually the same as was found in the first set of experiments. As the partition and thus the distance E was reduced from 48 to 27 cm VT_W did not show any change of efficiency in his visual acuity. For the stripe width of 0,8 mm, which VT_W could still discriminate, the visual angle was 10,2 minutes. VT_H, on the other hand, tended to choose one particular side increasingly as the experiment proceeded. This made a determination of the smallest visual angle impossible.

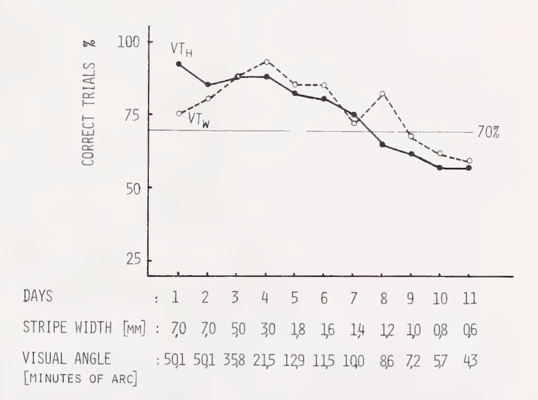


Fig. 5. Number of correct trials after the gradual reduction of the stripe width. (Day one means the first training day after learning the pattern discrimination)

There were great differences in how the animals behaved in the apparatus. Sometimes they were calm and attentive to the apparatus. In other instances, the test animal dashed around the apparatus in a hectic manner. An animal might rush into one of the choice alleys, realize his error, and then quickly turn around and go into the correct alley. A run of this sort was scored as a miss, even though after an initial error at the partition, the animal definitely made the right choice.

Discussion

Many physiological as well as psychological factors influence determination of visual acuity. Thus results of this study might not be directly comparable with the results of previous authors or investigations into other species. Methods of investigating visual acuity often vary considerably from author to author. Different intensities of illumination can produce differences in the results, as could be shown by Cavonius and Robbins (1973) with rhesus monkeys and Rahmann et al. (1968) with deermice (*Peromyscus*). Moreover, the willingness and ability to concentrate shown by the test animals plays a role (Rahmann 1967). Thus, the failure to perform, which occurred again and again in this study, both in the training apparatus and in the drum, might be the result of many factors including distraction, weariness, and stress of the test animals.

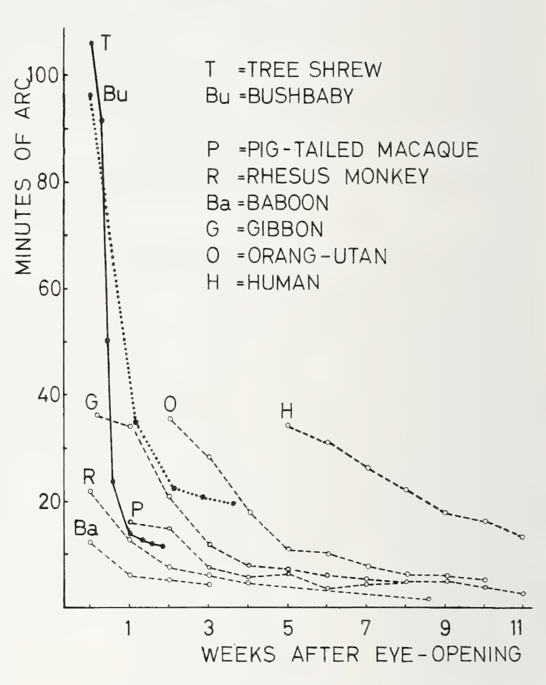


Fig. 6. Development of visual acuity in tupaias in comparison to that of some primates. (Treeshrews and bushbaby from own data, other data from Fobes and King 1982)

The value for visual acuity of 8,6 minutes of arc, which has been obtained with the adult tupaias in our training apparatus, is similar to the results of Schäfer (1969) found in a comparable discrimination apparatus for tupaias (visual acuity: 6,8 minutes of arc). Using a "noncorrection method of training", Ordy and Samorajski (1968) found a visual acuity of tupaias of 0,5 to 1,5 minutes of arc which appears quite high (Tab. 1).

Figure 6 shows the time course of the development of visual acuity in tupaias compared with that of some primates: tupaias and rhesus monkeys achieve some 14 minutes at an age of about one week after eye opening (rhesus and other primates: eyes are open at birth). Baboons show this value soon after birth (Fobes and King 1982). Pig-tailed macaques (*Macaca nemestrina*) pass the limit of 14 minutes after 2 to 3 weeks, gibbons after 3 weeks, orangs after 5 weeks and man after about 11 weeks (Fobes and King 1982). A bushbaby (*Galago senegalensis*; behaviourly investigated by Zimmermann 1987) tested with the same method, showed a visual acuity of 18,7 minutes after 25 days (end of the experiment). Obviously with increasing phylogenetic level, the speed of development of visual acuity slows down. This is consistant with the observation that the "higher" the phylogenetic

Table 1. **Visual acuity of treeshrews tested by different authors**

	This work	Schäfer (1969)	Ordy and Samorajski (1968)
Visual acuity (minutes of arc)	8 · 6	6 · 8	0 · 5 to 1 · 5
Apparatus	Two-alternative choice apparatus	Two-alternative choice apparatus	Two-alternative choice apparatus
Method	With reward, no punishment	With reward, with punishment (sudden noise)	With reward, a „non-correction method of training"

rank of a primate is, the longer its ontogeny takes. Tupaias, that independently leave their nest some 12 days after their eyes opened need a good visual acuity at that time to find their way through the environment, to catch small insects and to recognize dangers. The later an animal reaches independence, the less urgent is the need for rapid development of visual acuity. A human child, for example, only reaches the efficiency of an adult at an age of five years (Boothe et al. 1985).

In comparing the values for visual acuity between treeshrews and primates (Tab. 2), the primates show a better visual acuity than the measured acuity of tupaias (about 9 minutes of arc).

Table 2. **Visual acuity of treeshrews and some primates**

Treeshrews this work, other data from Fobes and King (1982)

Species	Visual acuity (minutes)
Treeshrews	8 · 6
Common marmosets	0 · 5 to 1 · 5
Cebus monkeys	0 · 95
Squirrel monkeys	0 · 86
Olive baboons	≤2 · 0
Pig-tailed macaques	3 · 4
Rhesus monkeys	0 · 65
Chimpanzees	0 · 47
Human beings	0 · 65

Acknowledgements

Thanks are due to Dr. S. K. Bearder, Anthropology Section, Oxford, and to Prof. Dr. B. Benson for checking the English style and for critical reading of an earlier version of this manuscript, to Prof. Dr. H. Sprankel, Department of Neuropathology, Gießen, for providing two pairs of *Tupaia belangeri* for founding the breeding stock of our University, to Dipl.-Ing. (FH) H. Oster, IBM Deutschland, for making the stripe patterns, to W. Kuttritz, Th. Plöttner and G. Tolkmitt for assisting in constructing the apparatus for the experiments and to W. Trumpp, G. Zander and T. Klesch for their permanent and indulgent support in maintaining the treeshrews in the animal house at Stuttgart-Hohenheim University.

Zusammenfassung

Die Entwicklung der Sehschärfe bei Spitzhörnchen (Tupaia belangeri)

Die ontogenetische Entwicklung der Sehschärfe wurde an 14 jungen Spitzhörnchen *(Tupaia belangeri)* ab dem Zeitpunkt des Augenöffnens (16. bis 23. Tag) bis zum Verlassen des Nests (30. bis 34. Tag) mit Hilfe einer optomotorischen Trommel getestet. Der erste optokinetische Nystagmus (OKN) trat zwischen dem 1. und 5. Tag nach dem Augenöffnen auf, dabei streuten die individuellen Sehschärfewerte beträchtlich (34,5 bis 370 Bogenminuten). Bis zum Verlassen des Nests pendelten sie sich auf etwa 11 Bogenminuten ein. Es zeigte sich eine Tendenz, daß mit zunehmender Dauer des Augenöffnens (wenige Stunden bis 3 Tage) eine Verzögerung des ersten Auftretens eines OKN einhergeht. Zwischen den Geschlechtern konnte in bezug auf die Sehschärfe kein Unterschied festgestellt werden. Zusätzlich wurde die Sehschärfe zweier adulter Tupaia-Männchen in einer 2-fach-Wahlapparatur bestimmt. Die ermittelte Sehschärfe lag bei 10 bzw. 8,6 Bogenminuten. Die Sehschärfewerte wurden mit denen einiger Primaten verglichen.

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Z. Säugetierkunde 53 (1988) 301–316

ISSN 0044-3468

Mécanismes de coexistence dans une guilde de muridés insulaires (*Rattus rattus* L., *Apodemus sylvaticus* L. et *Mus musculus domesticus* Rutty) en Corse: Conséquences évolutives

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Reception du Ms. 02. 04. 1987

Abstract

Mechanisms of coexistence in a guild of insular Murids (Rattus rattus L., Apodemus sylvaticus L., and Mus musculus domesticus Rutty) in Corsica: Evolutionary consequences

Studied the guild of Murids from the mediterranean island of Corsica (*Rattus rattus, Apodemus sylvaticus* and *Mus musculus domesticus*), in order to elucidate the relationships between its members and to propose potential evolutionary trends for them. The distribution of the three species at a regional scale is apprehended through extensive trapping throughout Corsica. The density fluctuations and the spatial distributions at a local scale are defined from a capture-recapture program in a North-Western locality of the island. Finally, the interindividual relationships between members of the three species are studied in the laboratory. Results indicate that the distribution and demography of the wood mouse is affected by the presence of the two other Murids, as are the activity patterns in captivity of both *A. sylvaticus* and *M. musculus* by the presence of *R. rattus* in captivity. Nevertheless, the coexistence of the three species is made possible by a shift of the demographic cycle of the wood mouse as well as of its habitat preference. This set of data suggests that the wood mouse, which was the first among the three species here studied to colonize Corsica, is also the one which suffers the most from interspecific interactions. This situation can lead *A. sylvaticus* to differentiate more rapidly, according to the "taxon" cycle theory of Mac Arthur and Wilson (1967).

Introduction

A la suite des travaux classiques de Mac Arthur et Wilson (1963, 1967), l'étude de la biogéographie insulaire s'est focalisée sur l'équilibre colonisations/extinctions. Pourtant, dans leur ouvrage paru en 1967, ces auteurs ont consacré un chapitre entier à l'évolution des populations insulaires («Evolutionary changes following colonization»), aspect par ailleurs largement discuté dans les ouvrages de Williamson (1981) et de Brown et Gibson (1983).

Constatant que les colonisateurs se recrutent essentiellement parmi les espèces habitant les milieux secondaires (milieux ouverts et instables, provenant généralement de la dégradation des milieux primaires, i.e. forestiers), Mac Arthur et Wilson (1967), reprenant les travaux de Wilson (1961) et de Carlquist (1966) sur les fourmis et les Composées du Pacifique, définissent un «taxon cycle» durant lequel l'évolution des communautés insulaires passe par trois phases:

1. colonisation des milieux secondaires par des espèces stratèges «r»;
2. pénétration des milieux forestiers par ces espèces, entraînant une perte du pouvoir de dispersion et un glissement vers une stratégie de type «K»;
3. différenciation aboutissant éventuellement à une spéciation souvent accompagnée d'une distribution relique.

Selon les cas, une recolonisation des milieux ouverts peut suivre une radiation adaptative, à moins que de nouveaux colonisateurs ne s'y soient déjà installés.

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Ce schéma a été par la suite appliqué avec succès aux avifaunes des Antilles par Ricklefs (1970) et Ricklefs et Cox (1972, 1978). Il insiste sur l'importance de la compétition interspécifique, qui repousse dans les milieux forestiers les colonisateurs primitifs, renforçant l'isolement de ces populations et leur évolution distincte (Mac Arthur et Wilson 1967: 157).

Brown et Gibson (1983) donnent plusieurs exemples empruntés aux oiseaux et aux lézards illustrant, selon eux, l'importance de la compétition interspécifique dans la distribution d'espèces insulaires.

Bien que l'importance même de la compétition ait été récemment remise en cause (Connell 1983; Schoener 1983; Bradley et Bradley 1985), les nombreux travaux réalisés sur des espèces du genre *Anolis* aux Antilles illustrent de façon pertinente la réalité de ce phénomène dans les groupes composés d'espèces affines, chez les Sauriens par exemple (Pacala et Roughgarden 1985; Rummel et Roughgarden 1985).

Les quelques analyses réalisées sur les communautés de Rongeurs aboutissent aux mêmes conclusions (Grant 1970; Crowell 1973, 1983; Crowell et Pimm 1976; Hallet 1982; Hallet et al. 1983; Dueser et Porter 1986), tout en mettant en évidence des différences selon les espèces étudiées. D'une façon générale, la compétition est d'autant plus intense que les espèces sont écologiquement, ou phylogéniquement, proches, ce qui confirme les prédictions du modèle théorique (Mac Arthur 1972).

La communauté de Rongeurs Muridés de Corse se prête bien à l'étude de ces processus évolutifs suivant la colonisation d'un milieu nouveau et des processus de compétition pouvant y être associés. Connaissant approximativement les modalités d'arrivée de ces espèces en Corse (Vigne 1983a et b), nous avons tenté de reconstituer le schéma de mise en place puis d'évolution de la guilde formée par le rat noir *(Rattus rattus)*, la souris domestique *(Mus musculus domesticus)* et le mulot sylvestre, *(Apodemus sylvaticus)*, à travers leur répartition actuelle dans l'île, leurs caractéristiques démographiques et spatiales au niveau d'une station, et enfin leurs relations interspécifiques en conditions de laboratoire.

Matériel et méthodes

Analyse écologique

Dans le but de connaître la répartition des trois Muridés en Corse, 22 stations de piégeage réparties sur tous les étages bioclimatiques de l'île entre 0 et 2064 m ont été échantillonnées de 1981 à 1985. La majorité de ces piégeages a été réalisée à l'aide de pièges grillagés de type Firobind. Les résultats permettent de préciser la répartition altitudinale des trois espèces de Muridés.

Par ailleurs, un quadrat de piégeage a été installé dans le vallon d'Elbo, situé dans la réserve naturelle de Scandola, au nord-ouest de la Corse (47,08 gr lat N; 6,93 gr long E). Ce quadrat comporte 94 jalons (76 en janvier 84), avec une maille de 20 mètres, l'ensemble couvrant une superficie de 3,76 ha (3,04 ha en janvier 84). Six sessions de capture ont été menées, en janvier, avril, juillet, octobre 1984, et en mars et juillet 1985. Durant ces périodes, les Rongeurs étaient piégés pendant 3 nuits successives, puis une quatrième nuit de capture, 3 jours plus tard, permettait d'estimer les densités de population grâce à l'indice de Lincoln. Deux pièges étaient installés à chaque jalon durant l'année 1984, un seul lors des deux sessions de 1985. Les pièges étaient appâtés à l'aide d'une pâte à base de farine, de sardines et d'huile d'olive, mélange qui s'est révélé attractif pour les trois espèces considérées ici. Les animaux capturés étaient marqués (amputation de phalanges ou bagues numérotées à l'oreille), sexés, pesés et leur état reproducteur était noté. Ils étaient ensuite relâchés à leur jalon de capture.

Les densités de population ont été estimées par l'indice de Lincoln, afin de faciliter les comparaisons avec la plupart des autres études (Orsini 1982; Cassaing et Croset 1985).

Parallèlement, un relevé de végétation a été effectué, en notant autour de chaque jalon la présence et l'abondance des espèces végétales présentes. Cinq zones ont pu alors être définies (Fig. 1). Ce sont:

Zone A: Friches à Graminées et petites Papilionacées, couvrant environ 1 ha dispersé en trois champs entourés de murs de pierres sèches. *Inula viscosa, Ferula communis, Euphorbia helioscopa* et divers *Plantago* en sont caractéristiques.

Zone B: Zones dégradées en adret sur sol rocheux, à *Cistus monspeliensis* et *Polygonum scoparium,* avec touffes de *Pistacia lentiscus.*

Zone C: Maquis (*Oleo-lentiscetum* climacique) à *Erica arborea, C. monspeliensis, P. lentiscus, Myrtus communis, Olea europaea, Phillyrea latifolia* et *Ph. angustifolia.*

Zone D: Maquis élevé à *Arbutus unedo* et *E. arborea* avec *Ph. latifolia* et *Viburnum tinus* (hauteur du toit de la formation: 2 m)

Zone E: Ripisylve dense à *P. lentiscus* avec *Ph. latifolia* et *V. tinus,* atteignant 2 à 3 m de haut. On y observe deux espèces d'arbres caractéristiques des ripisylves méditerranéennes chaudes: *Fraxinus ornus* et *Vitex agnus castus;* cette formation comporte par ailleurs de nombreuses lianes: *Rubus fruticosus* et *ulmifolois, Smilax aspera, Tamus communis, Clematis flammula* et *vitalba.*

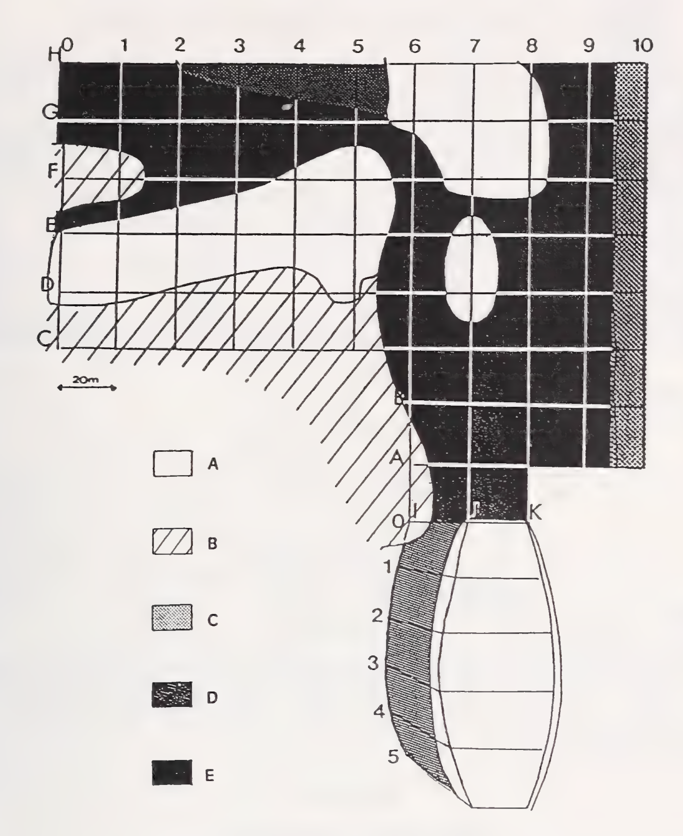


Fig. 1. Plan du quadrat de piégeage d'Elbo et des zones de végétation recensées

Les effectifs de capture de chaque espèce dans ces cinq milieux au cours des six sessions de piégeage ont permis de réaliser une analyse factorielle des correspondances afin de préciser la répartition spatio-temporelle de ces trois espèces sur le quadrat. Ensuite, la répartition de chaque espèce dans chacune de ces cinq zones a été exprimée en pourcentage du nombre total de captures de cette espèce au cours d'une période donnée. Les pourcentages de capture ainsi obtenus ont été rapportés à la surface occupée par ces zones de végétation exprimée en pourcentage de la surface totale du quadrat. Cet indice de répartition.

$$Ir = \frac{\text{\% capture sp N dans milieu M}}{\text{\% S occupé par M}}$$

a été calculé pour chaque espèce dans chaque milieu, d'une part lors de chacune des 6 sessions de piégeage, et d'autre part à l'aide de l'ensemble des résultats des 6 périodes réunies. Une valeur de Ir supérieure à 1 reflète donc une présence préférentielle de l'espèce dans le milieu considéré; une valeur de Ir proche de 1 signifie que l'espèce est présente dans le milieu de façon aléatoire; une valeur de Ir inférieure à 1 montre que la zone est plus ou moins délaissée par l'espèce.

Par ailleurs, les fréquences de capture des espèces dans les différentes zones de végétation ont

permis de déterminer deux paramètres importants de la niche écologique de ces espèces (BLONDEL 1979):

– L'amplitude d'habitat AH = $e^{H'}$, avec $H' = -\Sigma p_i \log_e p_i$ où p_i représente la fréquence de l'espèce dans le milieu i.

– Le barycentre $G = x_1 + 2x_2 + \ldots + nx_n / \Sigma x$, avec x_1, x_2, x_n représentant les abondances des espèces dans les milieux (n = 5 ici). Ce paramètre situe le préférendum écologique des espèces dans le gradient considéré.

Analyse des interactions interspécifiques en laboratoire

Les rythmes d'activité de souris et de mulots provenant de différentes localités, la plupart insulaires, ont été enregistrés en absence et en présence de congénères et de rats noirs. Pour ce faire, les animaux sont placés dans des cages individuelles reliées à un terrarium contenant nourriture et boisson ad libitum par l'intermédiaire de tubes (fig. 2). Sur ces tubes, sont placés des cellules photo-électriques reliées à un micro-ordinateur (REQUIRAND et al. 1987) enregistrant les passages des Rongeurs, ainsi que le temps qu'ils passent dans chacun des compartiments. L'indice d'activité pris en compte est le nombre de passage des cages individuelles au terrarium. Les résultats représentent des moyennes de trois à six jours d'expérience. Trois types d'enregistrement ont été effectués:
– rythme d'une souris ou d'un mulot seul dans le dispositif.
– rythme de souris ou de mulot en présence d'un individu de la même espèce.
– rythme d'une souris ou d'un mulot en présence d'un rat noir.
Dans cette dernière configuration, le tube permettant le passage de la souris ou du mulot de sa cage au terrarium a un diamètre suffisamment petit pour que le rat noir ne l'emprunte pas.

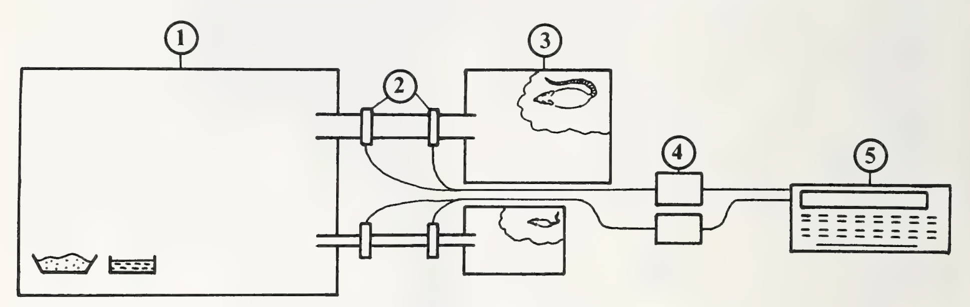


Fig. 2. Schéma du protocole expérimental d'enregistrement des rythmes d'activité de *M. musculus* et *A. sylvaticus* en présence ou absence de *R. rattus* ou d'un congénère; 1 = terrarium avec nourriture et boisson; 2 = compteurs de passage; 3 = cages individuelles; 4 = interface; 5 = micro-ordinateur enregistrant les données

Résultats

Répartition altitudinale

131 souris, 129 rats, 21 mulots et 4 lérots *(Eliomys quercinus)* ont été capturés au cours des 4124 nuits-pièges (n.p.) réalisées dans l'ensemble de la Corse. Deux espèces montrent une répartition semblable: *R. rattus* et *M. musculus domesticus* (Fig. 3). Ces deux espèces sont particulièrement abondantes dans les zones humides littorales, où leurs fréquences sont comparables (0,058 et 0,054 ind/n.p.). Ces chiffres diminuent rapidement dans les maquis de l'étage collinéen, où le rat est près de quatre fois plus abondant que la souris, puis ces deux espèces disparaissent progressivement vers 1000 m d'altitude. La répartition de *A. sylvaticus* est inversée par rapport à celle des deux autres Muridés: le mulot est généralement rare dans l'ensemble des étages méditerranéen et supra-méditerranéen, où ses abondances varient peu. Il devient relativement fréquent (0,015 ind/n.p.) dans l'étage subalpin, où les deux espèces précédentes sont absentes. Ces résultats correspondent étroitement avec ceux obtenus, dans l'île, par LIBOIS (1984), d'après l'examen de pelotes de la chouette effraie *(Tyto alba):* la fréquence du mulot est en effet trois fois plus faible dans les pelotes recueillies en-dessous de 500 m qu'en dessus de cette altitude, alors que l'inverse est vrai pour les deux autres Muridés. En Provence continentale, l'abondance du mulot

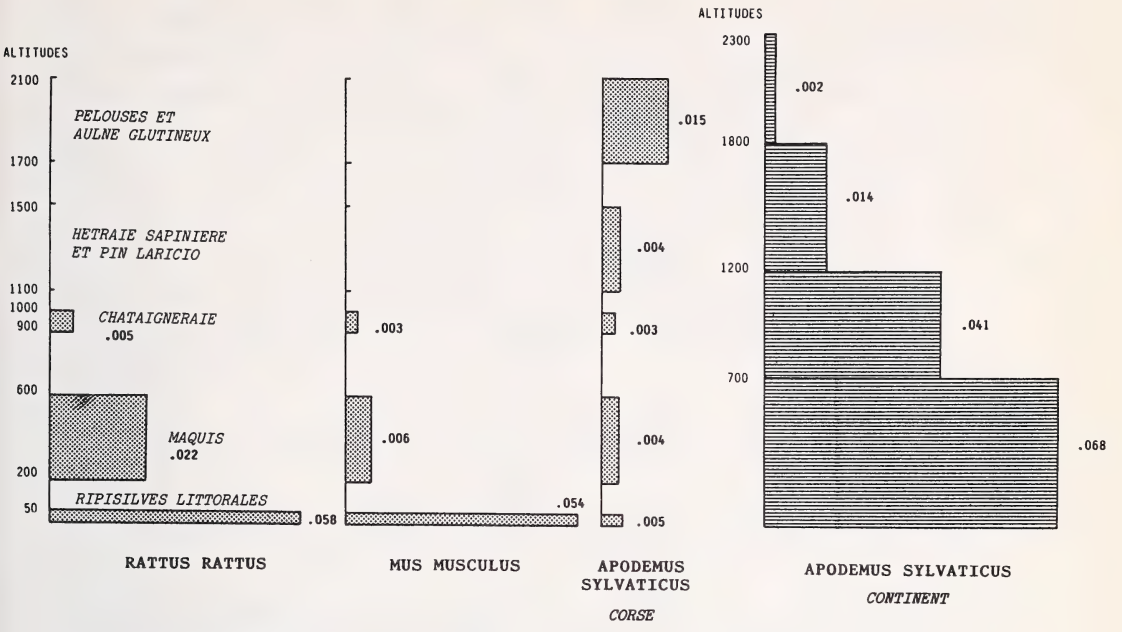


Fig. 3. Répartition altitudinale de *R. rattus*, *M. musculus* et *A. sylvaticus* en Corse, ainsi que d'*A. sylvaticus* sur le continent (d'après ORSINI 1981). Les fréquences sont exprimées en nombre de captures par nuit/piège

décroit régulièrement avec l'altitude: la densité de l'espèce est maximale dans les milieux méditerranéens (0,068 ind/n.p.) et minimale dans l'étage subalpin (0,002 ind/n.p., ORSINI 1981, cf fig. 3). La répartition altitudinale de cette espèce est donc complètement différente en Corse et sur le continent. Or, dans les milieux méditerranéens continentaux, *R. rattus* est généralement rare ou absent et n'est abondant que dans quelques secteurs chauds. On peut donc supposer que la distribution du mulot en Corse est influencée par celle du rat noir, dont la répartition est certainement dans cette île plus régulière que sur le continent, et les densités plus élevées.

Densités et variations d'abondance

Au cours des 6 sessions de piégeage réalisées sur le quadrat d'Elbo, 138 captures de rats, 175 de mulots et 338 de souris ont été enregistrées, soit respectivement 88, 84, et 140 individus différents de chaque espèce. Les densités des 3 Muridés estimées par l'indice de Lincoln à partir de ces effectifs capturés sont représentés sur la figure 4. Le cycle de la souris et celui du rat sont corrélés positivement ($r = 0{,}787$ $0{,}10 < p < 0{,}05$), alors que celui du mulot est corrélé négativement avec celui des deux autres espèces (avec souris $r = -0{,}236$; avec rat $r = -0{,}309$). Les chiffres obtenus varient, pour le mulot entre 1 et 12 individus par hectare, pour le rat noir entre 3 et 14 ind/ha et pour la souris entre 3 et 23 ind/ha. Par comparaison avec des données continentales obtenues dans les environs de Montpellier (Sud de la France) avec le même protocole, deux espèces apparaissent nettement plus abondantes en Corse que sur le continent (*M. musculus* et *R. rattus*), alors que les densités de l'autre *(A. sylvaticus)* y sont plus faibles: dans un milieu dunaire, les densités de souris varient de 0,5 à 7 ind/ha, alors que les densités de mulot fluctuent entre 9 et 28 ind/ha dans un milieu de garrigue (ORSINI 1982). En Camargue, les densités de rat noir ne dépassent pas 3 ind/ha (données non publiées).

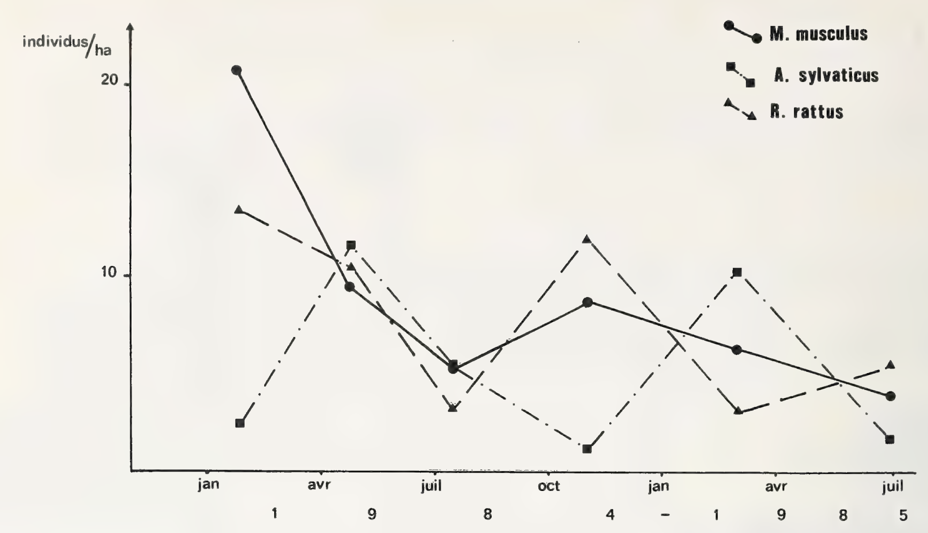


Fig. 4. Variations d'abondance de *R. rattus, M. musculus* et *A. sylvaticus* de janvier 1984 à juillet 1985 sur le quadrat d'Elbo (Corse). Les effectifs sont estimés par l'indice de Lincoln

Ainsi, les effectifs de rats et de souris sont-ils maximums en fin d'automne-début d'hiver, alors que ceux du mulot atteignent leur apogée au printemps. Pour cette dernière espèce, le cycle démographique réalisé en Corse est très différent de celui observé généralement sur le continent, en région méditerranéenne: 3 populations de mulots, suivies entre 1979 et 1981 dans trois biotopes continentaux différents des environs de Montpellier (France), montrent des pics de densité essentiellement hivernaux (Orsini 1982). Dans ces trois situations, les souris (*Mus musculus domesticus* ou *Mus spretus* ou les deux) sont les seuls autres Muridés présents en effectifs comparables, le rat noir y étant absent. De même, en Camargue, en absence de compétiteur, les densités maximales de mulots sont nettement hivernales (Jamon 1986).

A l'opposé, les variations annuelles d'effectifs observées chez la souris à Elbo sont du même type que dans les populations continentales de l'espèce (Orsini 1982; Boitani et al. 1985; Navajas 1986). Les données concernant le rat noir sur le continent montrent une grande variabilité des cycles de densité réalisés (Davis 1953). Dans d'autres îles méditerranéennes, les densités de cette espèce semblent en général assez fortes en hiver, en présence ou non d'autres Muridés; la saison de reproduction est de plus beaucoup plus étalée en Corse que dans les petites îles (Cheylan 1986), ce qui permet au rat noir de voir sa population se reconstituer plus rapidement que celle des deux autres espèces à Elbo (cf. Fig. 4), après le très sévère hiver 1984/1985.

Répartition spatiale

La figure 5 montre que la discrimination spatiale des trois espèces est globalement très nette, quelle que soit la période considérée, à part en janvier 1984 (période 1) où rat noir et mulot ont des distributions semblables.

Dans le détail, et au vu des histogrammes de la fig. 6, il apparaît que:

a. le rat noir est, à toutes les périodes à l'exception de Janvier 1984 (Ir = 0,94), capturé préférentiellement dans la zone E, zone de recouvrement végétal maximum (Ir = 1,84 à 2,10). Ceci se retrouve donc dans le schéma global, prenant en compte toutes les sessions de capture (Ir = 1,53). Les autres milieux sont plus ou moins délaissés, à part le milieu C, fréquenté de façon irrégulière selon les saisons.

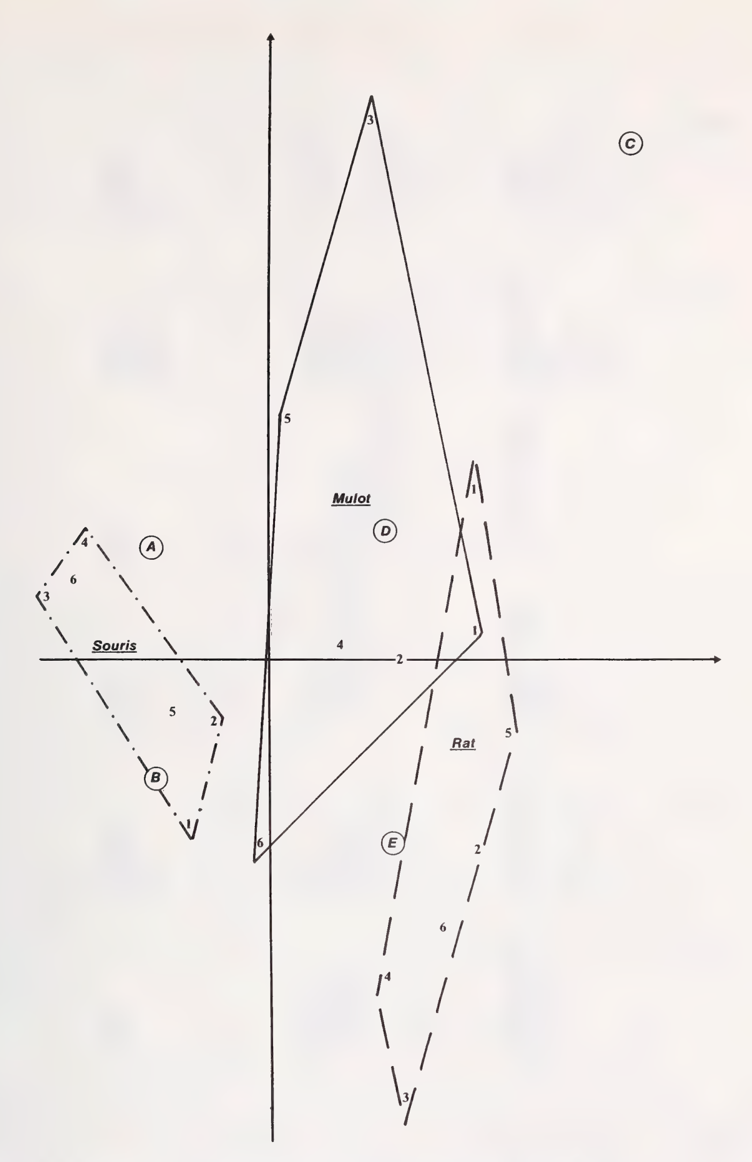


Fig. 5. Plan 1 × 2 de l'AFC réalisée à partir des nombres de captures de *R. rattus, M. musculus* et *A. sylvaticus* dans les 5 zones de végétation (A à E) du quadrat d'Elbo (cf Fig. 1), au cours des 6 sessions de piégeage (1 à 6)

b. la souris domestique est systématiquement ou presque sur-représentée dans les milieux A (1,21 < Ir <2,02) et B (0,74 < Ir <1,58), les deux milieux les plus ouverts. Elle est pratiquement absente de la zone C, très rocheuse et se retrouve dans les zones D et E mais à des effectifs assez faibles (Ir = 0,50 et 0,74 respectivement, sur l'ensemble des sessions).

c. le mulot apparaît globalement bien représenté dans tous les milieux (0,73 < Ir <1,36 pour les cinq zones, toutes sessions confondues), mais ceci traduit des abondances très variables dans chaque zone selon la période de capture. Ainsi, il est recontré préférentielle-

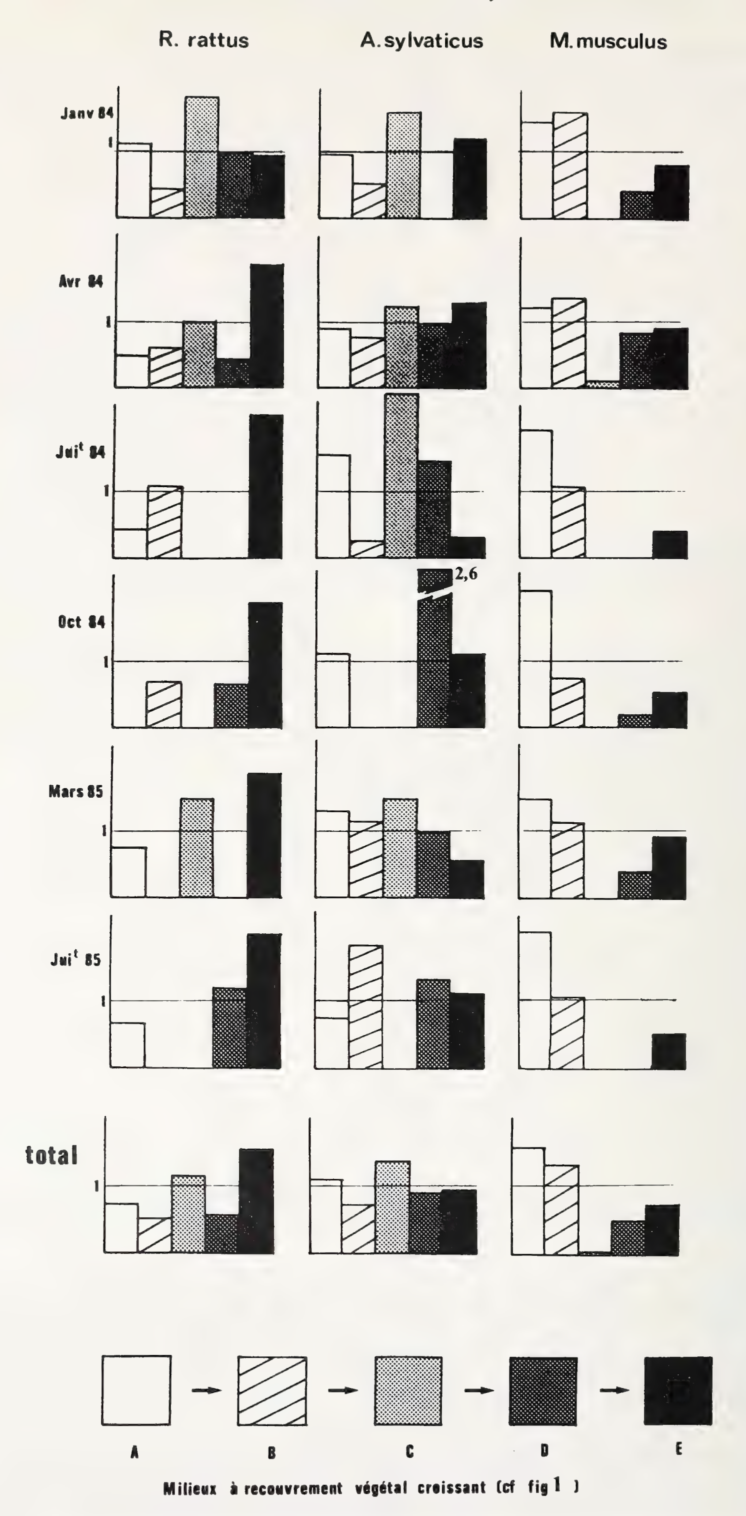


Fig. 6. Indices de répartition (Ir, cf texte) par zone de végétation, de *R. rattus, M. musculus* et *A. sylvaticus* sur le quadrat d'Elbo (Corse)

ment dans la zone C en janvier et juillet 1984, dans la zone D en octobre 84 et dans la zone B en juillet 85. Il parait donc très ubiquiste, avec un léger préférendum pour les milieux à recouvrement végétal intermédiaire.

Le rat noir apparaît finalement comme l'espèce la plus forestière, avec un barycentre (G) de 3,6 (Tab. 1), alors que la souris est caractéristique des milieux ouverts (G = 2,3). Le mulot est l'espèce qui présente l'amplitude d'habitat la plus grande (AH = 4,2 contre 3,5 et 3,1 aux deux autres espèces).

Tableau 1. **Amplitude (AH) et barycentre (G) d'habitat de *R. rattus, M. musculus* et *A. sylvaticus* sur le quadrat d'Elbo**

	R. rattus	A. sylvaticus	M. musculus
AH	3,48	4,16	3,14
G	3,58	2,93	2,34

Rythmes d'activité en captivité

Dans tous les cas, le rythme d'activité des rats noirs testés s'est montré indépendant de la présence ou non d'un individu d'une autre espèce. Il n'est pas non plus apparu de différences entre les rythmes d'activité des souris et des mulots seuls ou avec un conspécifique. Par contre, le comportement des souris (N = 4) et mulots (N = 4) a été diversement affecté par la présence d'un rat.

En ce qui concerne la souris (Fig. 7), on observe généralement une réduction de l'activité d'un facteur 2 en présence du rat noir, et/ou, dans deux cas, un décalage de l'activité vers le matin. Ces différences sont dans deux cas significatives (test de Wilcoxon, Siegel 1956). Dans un cas la souris a été finalement tuée par le rat, le troisième jour de l'expérience.

Les rythmes d'activité des mulots testés ont été très perturbés par la présence du rat noir (Fig. 8): dans deux cas, on observe une diminution d'un facteur 2 et dans un cas une augmentation d'un facteur 7 de la quantité d'activité. Ces différences sont toutes significatives. Dans 3 cas sur 4, le mulot a été tué et partiellement dévoré par le rat au bout de 3 ou 4 jours d'expérience.

Discussion

Plusieurs auteurs ont insisté sur l'appauvrissement spécifique qui caractérise les peuplements insulaires (Mac Arthur et Wilson 1967; Blondel 1979, 1986; Williamson 1981; Brown et Gibson 1983). Cet appauvrissement est souvent compensé par l'augmentation de densité des espèces présentes, généralement bien plus abondantes dans les îles que sur le continent.

Ainsi, l'appauvrissement spécifique du peuplement mammalien de la Corse est important: par rapport à des zones homologues du continent, 62 % des espèces manquent en Corse, la communauté de Rongeurs ne comptant que 6 espèces (Cheylan 1984); celles-ci se répartissent en 4 Muridés (*Rattus norvegicus* plus les 3 espèces étudiées ici) et 2 Gliridés (*Glis glis* et *Eliomys quercinus*). Toutefois, les répartitions de 2 de ces espèces (*R. norvegicus* et *G. glis*) sont très ponctuelles, alors que les autres sont assez bien réparties dans la plupart des milieux de l'île (Salotti 1984). On peut donc s'attendre à trouver dans cette île une compensation de densité affectant ces 4 espèces.

Effectivement, on constate que les abondances du rat et de la souris sont plus élevées en Corse que dans des biotopes similaires du Midi de la France et d'Italie, alors que les

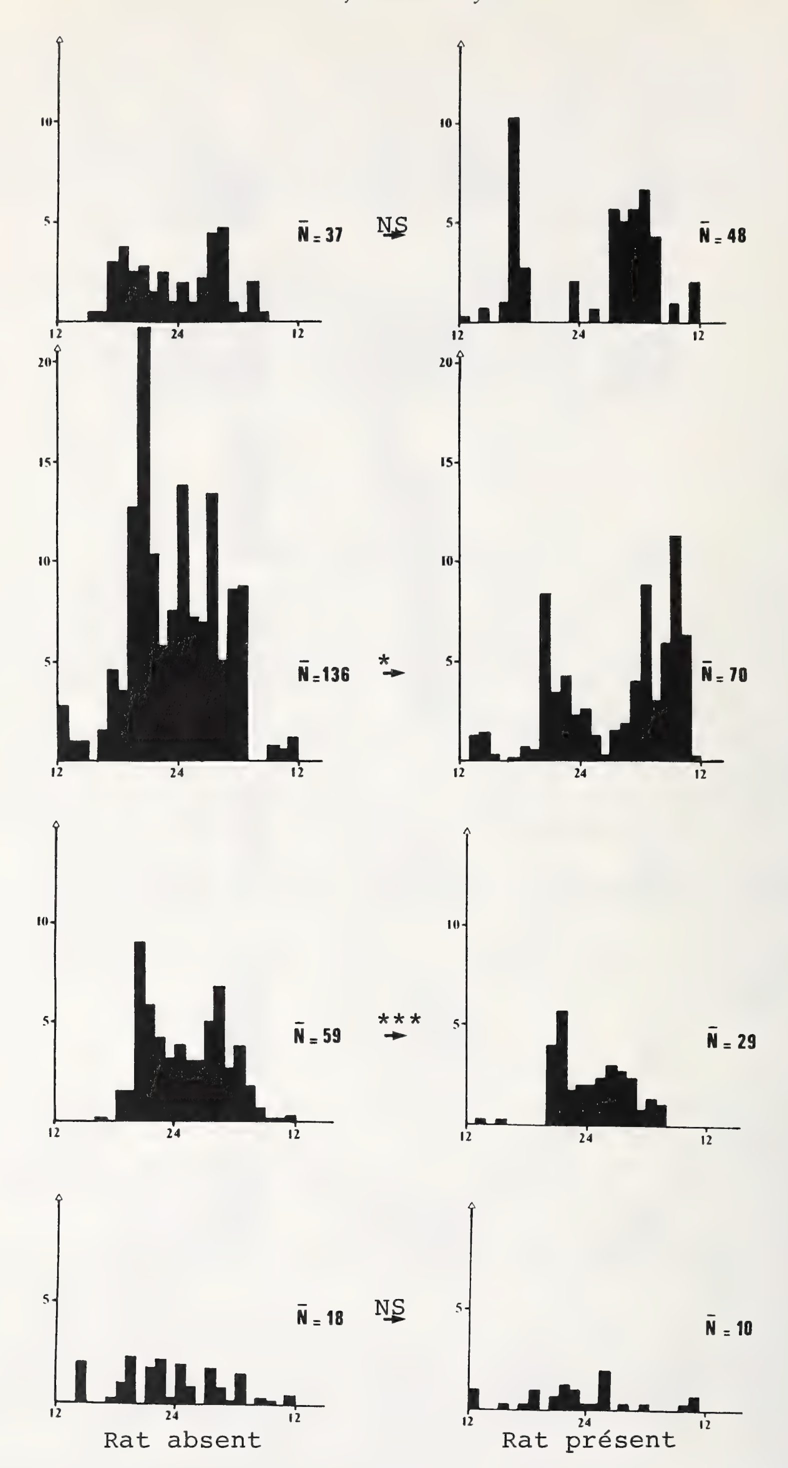


Fig. 7. Rythmes d'activité de souris (N = 4) en absence et en présence de rat noir (abscisse: heures; ordonnée = nombre de passages. Test de Wilcoxon: NS = non significatif; $^{*}p < 0{,}05$; $^{***}p < 0{,}001$)

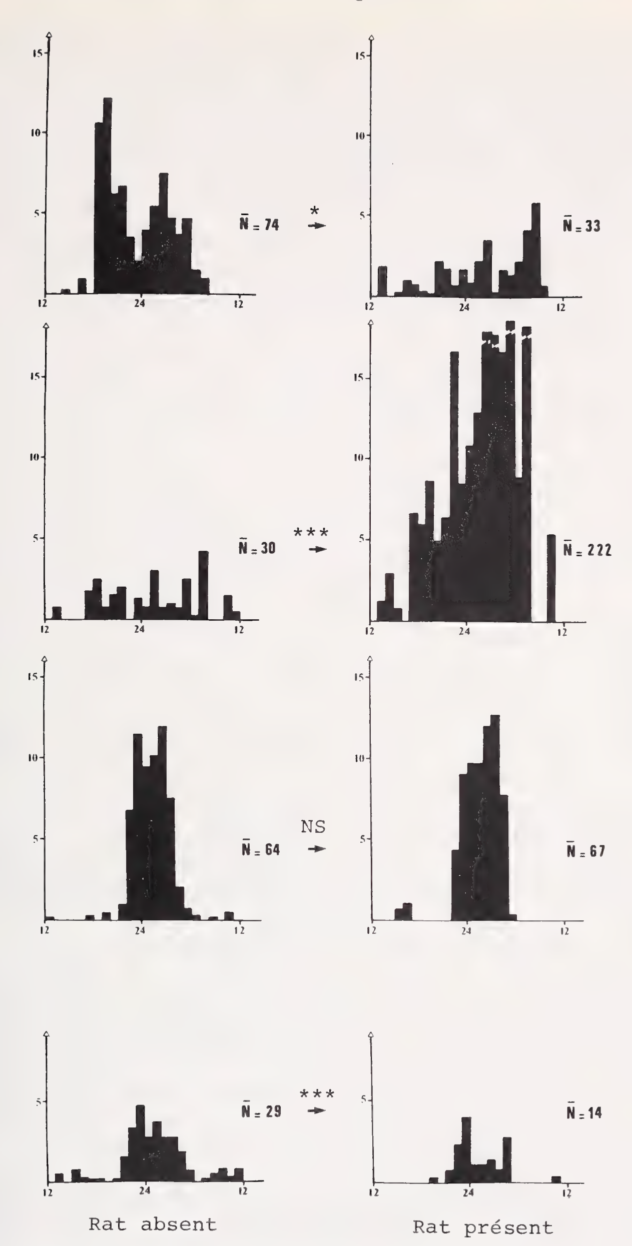


Fig. 8. Rythmes d'activité de mulots (N = 4) en absence et en présence de rat noir (même légende que pour la souris)

abondances du mulot sont comparables (ORSINI 1982; CASSAING et CROSET 1985; BOITANI et al. 1985; NAVAJAS 1986; CHEYLAN 1986). Ces augmentations de densités insulaires sont généralement attribuées à une diminution des pressions de prédation et de compétition interspécifique (LIDICKER 1973; TAMARIN 1977; CHEYLAN et GRANJON 1985). En l'absence d'augmentation de densité chez *A. sylvaticus,* on peut penser que les pressions de compétition interspécifique vis-à-vis de cette espèce ne se sont pas relâchées dans le secteur

d'étude, la prédation pouvant être par ailleurs considérée comme s'exerçant de la même façon sur les trois espèces, ou tout au moins sur le mulot et la souris, de taille comparable.

Le décalage temporel du cycle démographique du mulot par rapport à celui des deux autres Muridés est du même type que celui recontré en Italie entre *M. musculus domesticus* et *A. sylvaticus* par Boitani et al. (1985), dans un milieu littoral où vit également *R. rattus* (Boitani, comm. pers.). Pour ces auteurs, ce mécanisme aurait pour but de réduire la compétition entre les deux espèces et aurait donc un caractère adaptatif. Dans notre cas, le même phénomène peut être invoqué, pour permetre la coexistence équilibrée des trois espèces. Le rat noir doit être le responsable du décalage du cycle démographique du mulot par rapport à ce qu'il est habituellement dans les biotopes méditerranéens continentaux où *Rattus rattus* est absent (Orsini 1982; Jamon 1986).

Un autre mécanisme qui semble entrer en jeu pour favoriser la coexistence entre les Muridés est la ségrégation spatiale de l'habitat. En effet, les trois espèces étudiées se répartissent différemment dans le gradient de milieux défini (Fig. 5 et 6): *Mus musculus* est beaucoup plus abondante dans les milieux ouverts, ce qui confirme ce que l'on sait des habitudes écologiques de cette espèce, liée le plus souvent aux milieux à faible recouvrement arbustif et arboré (Orsini 1982; Orsini et al. 1982; Boitani et al. 1985). *Rattus rattus* est quant à lui plus fréquemment capturé dans les zones boisées qui constituent son habitat préférentiel, puisqu'en région méditerranéenne continentale, il est inféodé à la forêt où il est souvent arboricole (Saint-Girons 1973). Le mulot est généralement très ubiquiste, mais montre lui aussi une préférence pour les milieux assez forestiers (Corbet 1966; Niethammer et Krapp 1978). En région méditerranéenne continentale, dans un biotope hétérogène et en présence de *Mus spretus,* il apparaît également lié à un couvert végétal important: garrigue à chêne kermès *(Q. coccifera)* et taillis à chêne vert *(Q. ilex)* (Orsini 1982). En revanche, il est assez bien réparti sur l'ensemble des milieux définis à Elbo, alors que son optimum d'habitat se rapprocherait de celui de *R. rattus.* Il semble donc que *A. sylvaticus* abandonne à Elbo les milieux les plus fermés pour se retrouver dans les milieux intermédiaires et même ouverts. Celà est possible grâce à ses capacités à vivre dans des habitats très divers ce que confirme ici sa grande amplitude d'habitat (Tab. 1), qui n'est cependant pas supérieure en Corse à ce qu'elle est sur le continent, contrairement aux deux autres Muridés (Libois 1984). C'est là encore le rat noir qui semble à l'origine de la répartition observée du mulot dans la zone d'étude.

La différenciation temporelle (décalage des cycles démographiques) et spatiale (ségrégation différentielle de l'habitat) entre les trois Muridés du vallon d'Elbo, en permet sans doute une exploitation mieux équilibrée des diverses ressources. Cette différenciation de niches est attestée par les nombres assez réduits de captures de deux individus d'espèces différentes au même jalon la même nuit, par rapport aux chiffres attendus sous l'hypothèse d'une répartition aléatoire des individus sur l'ensemble du quadrat à chaque session de piégeage (tab. 2): l'évitement mulot-rat est maximum alors que ce sont les deux espèces les plus susceptibles de se rencontrer, d'après leur répartition sur le quadrat (cf. Fig. 5 et 6).

Tableau 2. **Nombres théoretique et observé de captures au même jalon et la même nuit de 2 Muridés d'espèces différentes sur le quadrat d'Elbo ($X^2 = 27{,}7$; p 0,001)**

	Rat Mulot	Rat Souris	Mulot Souris
Nombre Théorique	11	26	33
Nombre Observé	1	13	13

Le mécanisme à l'origine de la ségrégation spatio-temporelle des trois espèces pourrait être de nature comportementale. L'influence de la présence du rat noir sur l'activité des deux autres Muridés montre que ces dernières espèces sont amenées à développer en

captivité des mécanismes d'évitement (déplacement ou réduction de l'activité) pour pouvoir cohabiter avec le rat noir. Il apparaît même dans ces conditions qu'un rat noir est capable du tuer assez rapidement un mulot ou une souris partageant son espace vital, le mulot semblant particulièrement devoir souffrir d'une telle promiscuité ce qui confirme les faits observés dans le milieu naturel, où le décalage des cycles démographiques permet cette coexistence, de même que la possibilité d'occuper des micro-habitats différents. Terman (1974) montre par exemple que la cohabitation de *Sigmodon hispidus* et *Microtus ochrogaster* en captivité est possible seulement si le milieu est complexifié par adjonction de fragments de papiers. Dans ce cas toutefois, les déplacements de *M. ochrogaster* sont beaucoup réduits par la présence de *S. hispidus.* De même, les déplacements du mulot en Corse sont particulièrement faibles par rapport à ce qui a été observé dans un milieu continental similaire, et avec le même protocole: (Distance Maximale de Recapture = 16 m à Elbo, 37 m vers Montpellier, Sud de la France, Orsini 1982).

A la suite d'une étude de plusieurs guildes de micromammifères déserticoles syntopiques, Hallet (1982) et Hallet et al. (1983) proposent un mécanisme selon lequel les espèces les plus généralistes seraient également les moins bonnes compétitrices et verraient leur amplitude d'habitat se réduire lors de l'augmentation de densité des espèces plus spécialisées et meilleures compétitrices, hypothèse tout à fait cohérente avec le «taxon cycle» de Mac Arthur et Wilson (1967). Dans le cas de la guilde des Muridés corses, *A. sylvaticus,* l'espèce la plus généraliste, paraît effectivement être le «moins bon» compétiteur des trois espèces en présence: il est dominé nettement par le rat noir, et les expériences de confrontation avec *A. flavicollis* (Hoffmeyer 1973; Montgomery 1978) montrent qu'il peut également l'être par une espèce de taille comparable à la sienne.

A l'issue de cette approche des relations interpopulationnelles et interindividuelles à différentes échelles de perception, on peut tenter de préciser le schéma connu de la colonisation puis de l'établissement d'*Apodemus sylvaticus, Rattus rattus* et *Mus musculus* en Corse.

Au cours du Pléistocène et du tout début de l'Holocène, la communauté de Rongeurs de la Corse n'est composée que de deux espèces endémiques: *Rhagamys orthodon* (Muridé) et *Thyrrenicola henseli* (Microtidé) (Vigne 1983a et b). Ces deux espèces persistent jusqu'à la fin du premier Millénaire BC et coexistent donc pendant 3000 ans avec *A. sylvaticus,* qui apparaît dans l'île au début du 3ème Millénaire BC.

En revanche, *R. rattus* n'est signalé qu'au 6ème siècle après J.C. (Vigne et Maringal-Vigne 1985), alors qu'aucun reste fossile de *Mus* n'est connu en Corse. Néanmoins, ces deux espèces pourraient avoir colonisé l'île plus tôt que ne l'indiquent les données paléontologiques actuellement disponibles, car elles sont signalées entre le Néolithique et l'époque romaine dans plusieurs îles de Méditerranée (Minorque: Reumer et Sanders 1984; Sardaigne: Sanges et Alcover 1980; Malte: Storch 1970).

Etant donné la taille de *Rhagamys* et *Thyrrenicola,* que l'on peut estimer à environ 50 g (Michaux, comm. pers.), il est probable que ces espèces pouvaient dominer *Apodemus* en condition de syntopie. Les restes fossiles de ces deux Rongeurs sont d'ailleurs abondants dans les gisements jusqu'à la fin du 1er millénaire, alors qu'*Apodemus* n'a livré que peu de restes osseux de cette époque. La colonisation de la Corse par cette espèce aurait donc pu être assez lente. Par contre, la disparition rapide et simultanée des deux espèces endémiques est plus ou moins concomitante à l'expansion géographique de *R. rattus* en Europe (Armitage et al. 1984). Parmi les différentes causes de l'extinction de *Rhagamys* et *Thyrrenicola* revues par Vigne (1983), l'apparition dans l'île de *R. rattus* pourrait bien être la principale.

Au cours de ses 5000 ans de présence dans l'île, *Apodemus sylvaticus* a donc toujours été dominé par des espèces de taille supérieure à la sienne, espèces qui exerçaient, ou qui exercent, une pression de compétition importante sur ses populations.

Néanmoins, pour des raisons liées à leurs origines biogéographiques, il est peu probable

que *M. musculus* et *R. rattus*, espèces thermophiles, puissent coloniser à court terme les biotopes forestiers montagnards à climat froid habités par *A. sylvaticus, E. quercinus,* et dans une moindre mesure, *G. glis.*

A. sylvaticus est donc la seule espèce, dans la guilde des Muridés corses, pouvant habiter les milieux forestiers de moyenne altitude caractérisés par un relâchement de la compétition. Elle représente donc, dans la théorie du «taxon cycle», le meilleur candidat à une différenciation insulaire, ce qui a été vérifié par une étude biométrique portant sur 26 caractères crâniens et corporels, comparant les populations de 4 Rongeurs de la Corse et du Midi de la France: *A. sylvaticus, M. musculus, R. rattus* et *E. quercinus* (Orsini et Cheylan 1983). Cette étude a révélé que la différenciation morphologique la plus poussée était atteinte par *Apodemus,* chez qui tous les caractères étudiés sont plus grands en Corse que sur le continent, alors que les trois autres espèces étudiées ne sont en général différenciées que sur des caractères de l'appareil manducateur. Libois et al. (1983), dans une comparaison entre les mulots de Corse et de la Belgique obtiennent des résultats comparables. Ceci est d'autant plus significatif que le groupe *A. sylvaticus/A. flavicollis* en Europe sud-occidentale se caractérise par une grande stabilité morphologique au cours des 3 derniers millions d'années (Michaux 1983).

Ces résultats corroborent donc les prédictions du modèle de Mac Arthur et Wilson (1967). La répartition très étendue mais fractionnée d'*Apodemus sylvaticus* dans l'île entraine sans doute une réduction des flux géniques, alors que les populations de *Rattus rattus* et, dans une moindre mesure, de *Mus musculus,* limitées à la ceinture de milieux méditerranéens qui entoure les montagnes de l'île, sont soumises à des échanges géniques plus intenses qui ralentissent leur différenciation.

Remerciements

Ces recherches ont été partiellement financées par le Parc Naturel Régional de Corse, grâce à son Directeur, M. Leenhardt, que nous tenons à remercier ici. Notre reconnaissance va également à J. C. Thibault, J. M. Casta, J. M. Caillaud et C. H. Bianconi pour leur appui lors des missions dans l'île, de même qu'à R. Fons, J. P. Clara, O. Pouliquen, M. Navajas, J. C. Auffray, A. Clamens et H. Gaubert qui ont participé au travail de terrain. P. Orsini nous a confié ses notes de piégeage qui ont permis de préciser la répartition des espèces dans l'île. J. Blondel, J. Cassaing et J. Michaux nous ont fait part de leurs remarques et nous les en remerciont vivement, ainsi que H. Croset, initiateur des ces recherches.

Résumé

La guilde des Muridés de Corse, formée du rat noir *(Rattus rattus)*, du mulot sylvestre *(Apodemus sylvaticus)* et de la souris domestique *(Mus musculus domesticus)* est étudiée à trois niveaux de perception différents: A l'échelle régionale, la répartition altitudinale du mulot est très différente de celle qu'il a sur le continent en région méditerranéenne. Au niveau stationnel, une étude sur quadrat de piégeage montre que le cycle d'abondance du mulot est décalé par rapport à celui des deux autres Muridés et par rapport à ce qu'il est sur le continent. D'autre part, les répartitions spatiales des trois espèces sont complémentaires, chacune étant préférentiellement rencontrée dans un type donné d'habitat. Enfin, les résultats de tests en captivité font apparaître une influence négative nette du rat noir sur l'activité des deux autres espèces. Cet ensemble de données suggèrent que la coexistence entre les trois espèces n'est possible que grâce à un ajustement de leurs distributions temporelle et spatiale. Par ailleurs, le mulot qui a été le premier colonisateur de la Corse parmi ces trois espèces, semble être actuellement l'espèce qui s'est le plus différenciée. La compétition avec les deux autres espèces pourrait être à l'origine de cette évolution.

Zusammenfassung

Mechanismen der Koexistenz von Insel-Muriden (Rattus rattus L., Apodemus sylvaticus L. und Mus musculus domesticus Rutty) auf Korsika: Evolutionäre Konsequenzen

Untersuchungen an den drei Muriden-Arten *Rattus rattus, Apodemus sylvaticus* und *Mus musculus domesticus* wurden auf Korsika (Frankreich) durchgeführt. Es ergaben sich folgende Ergebnisse: Die Höhenverteilung in der Häufigkeit des Auftretens unterscheidet sich bei *Apodemus sylvaticus* auf Korsika stark von der auf dem mediterranen Festland. Auch die jahreszeitliche Abundanz-Änderung

dieser Art weicht von der auf dem Festland ab und darüber hinaus auch von jener der beiden anderen Muriden-Arten auf Korsika. Die drei Arten besiedeln bevorzugt Habitate, die einander ergänzen. Versuche in Gefangenschaft zeigten, daß *Rattus rattus* die Aktivitäten der beiden anderen Arten herabsetzt. Offenbar bestimmt die auf Korsika im Vergleich zum Festland häufigere Hausratte die dort andersartige Verteilung der Waldmaus. *Apodemus sylvaticus,* der erste Einwanderer unter diesen drei Arten, ist dieser interspezifischen Konkurrenz am stärksten und in besonderer Weise ausgesetzt. Möglicherweise ist aus entsprechenden Gründen in erster Linie *Rattus rattus* verantwortlich für den Zusammenbruch von Populationen und das Verschwinden der endemischen Muriden, die bis 1000 v. Chr. auf Korsika gelebt haben.

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Z. Säugetierkunde 53 (1988) 317–319

ISSN 0044-3468

WISSENSCHAFTLICHE KURZMITTEILUNG

Weitgehende Rotation des 4. Prämolaren im Unterkiefer eines Rothirsches (*Cervus elaphus* L.) und eines Rehbockes (*Capreolus capreolus* L.)

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Eingang des Ms. 01. 02. 1988

Als Zahnrotation (Rotatio dentis) bezeichnet man eine Stellungsanomalie, bei der ein Zahn um seine Längsachse gedreht ist. Im folgenden werden zwei Fälle sehr weitgehender Rotation des mandibularen 4. Prämolaren bei Cerviden beschrieben.

Bei dem ersten Objekt handelt es sich um die linke Unterkieferhälfte eines Rothirsches *(Cervus elaphus)*, dessen Alter nach dem Zahnabschliff auf 6–7 Jahre geschätzt wird. In der mit 11,96 cm (Messung an Kronenbasis) normal langen Backenzahnreihe (Bützler 1986) ist der P_4 um 180° rotiert, so daß seine morphologische Buccalseite nach lingual weist (Abb. 1). Die (typisch geformte) Krone des Zahnes ist gegen die Wurzel buccalwärts abgebogen (Buccaldeviation der Zahnkrone) und schert daher leicht aus der Backenzahnreihe aus. Eine Torsion, d. h. eine Verdrehung der Wurzel gegenüber der Zahnkrone, tritt jedoch nicht auf. Der rotierte P_4 kann nicht aus seiner Alveole herausgezogen werden, da die Wurzelspitzen, wie Röntgenaufnahmen zeigen, mesialwärts umgebogen sind. Die mesiale und distale Kronenfläche dieses Zahnes sowie die Approximalflächen der angrenzenden P_3 und M_1 zeigen deutliche Abnutzungsspuren.

Als zweites Objekt liegt die rechte Unterkiefer-Backenzahnreihe eines etwa zweijährigen Rehbockes *(Capreolus capreolus)* vor, deren Länge mit 6,16 cm (Messung an Kronenbasis) innerhalb der für diese Art festgestellten Variationsbreite liegt (Lehmann und Sägesser 1986, eigene Befunde). In diesem Fall beträgt die Rotation des P_4 etwa 140° (Abb. 2), so daß die Distalfläche des Zahnes mesiobuccalwärts weist. Zwischen ihm und den benachbarten Zähnen haben sich infolge approximaler Abnutzung distinkte Kontaktflächen ausgebildet. Die Krone des gedrehten Zahnes ist normal gestaltet.

Das Auftreten von Rotatio dentis ist in der odontologischen Literatur vielfach belegt (Eidmann 1939; Garlick 1954; De Jonge 1965; Becker 1970; Pindborg 1970; Meyer 1975; Vigal und Machordom 1987). In der Regel beträgt die Drehung maximal 90° und tritt zumeist als Folge einer zu engen Zahnstellung auf. Auch durch Hypodontie oder posteruptiven Zahnverlust ausgelöste Migration einzelner Zähne kann zur Entstehung derartiger Stellungsanomalien führen.

Zahnrotationen von mehr als 90° in vollständigen Zahnreihen sind demgegenüber sehr selten. Im menschlichen Gebiß zeigt nach De Jonge (1965) am häufigsten der P^2 eine solche Veränderung, die gelegentlich auch bilateral-symmetrisch auftreten kann.

Für Cerviden liegen nur wenige Mitteilungen über weitgehende Zahnrotationen vor. Eidmann (1939) schildert die Drehung des linken I_1 um 180° bei einem Rothirsch. Bei der gleichen Art beschreiben Pucher (1983) und Wollenhaupt (1986) jeweils eine 180° betragende Rotation des linken P_2. Belegt wird die sehr geringe Frequenz des Auftretens dieser Aberration durch die Tatsache, daß bei der von den Verfassern im Rahmen einer

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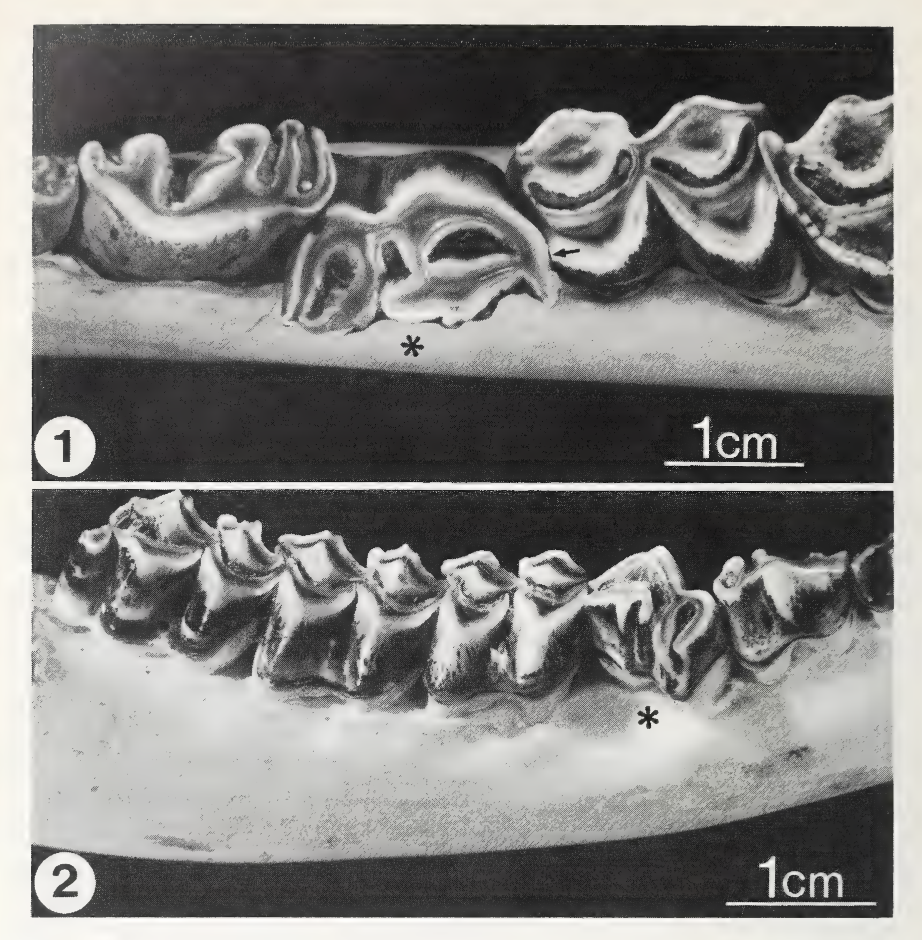


Abb. 1. Um 180° gedrehter linker P_4 (*) eines Rothirsches. Ansicht von okklusal. Beachte Abnutzung der approximalen Zahnflächen (Pfeil) – *Abb. 2.* Um ca. 140° rotierter P_4 (*) in der rechten Unterkiefer-Backenzahnreihe eines Rehbockes. Ansicht von bucco-okklusal

anderen Untersuchung (KIERDORF und KIERDORF 1986) durchgeführten Überprüfung von ca. 10 000 Reh-Unterkiefern einzig der hier dargestellte Fall beobachtet wurde.

Die Ursachen der über 90° hinausgehenden Zahnrotationen sind zur Zeit noch nicht geklärt. DE JONGE (1965) stellt sie mit Recht als Anomalien besonderer Art heraus, die nicht als Folge von Raummangel im Zahnbogen erklärt werden können. In diesem Zusammenhang ist auf die Untersuchungen von OOË (1962, 1968) am menschlichen Gebiß und von ESAKA (1982) an demjenigen dolichocephaler Hunde hinzuweisen. Danach führen die Zahnkeime im Normalverlauf der Odontogenese bereits auf dem Knospen- und Kappenstadium Rotationsbewegungen aus. Dies geschieht während einer Entwicklungsphase, in der zwischen den einzelnen Anlagen noch ausreichende Zwischenräume vorhanden sind. Die Rotationen lassen sich daher nach Ansicht der genannten Autoren nicht auf Platzmangel zurückführen, sondern sind Folge autonomer Bewegungstendenzen der Zahnkeime. Im Zuge der Normalentwicklung werden die Drehungen gegenüber der definitiven Position der Zähne im Kiefer später rückgängig gemacht. Vermutlich liegt den beschriebenen Zahnstellungsanomalien eine Störung der oben geschilderten Vorgänge zugrunde.

Danksagung

Für die Überlassung des Materials danken die Verfasser Herrn L. v. Lüninck, Bourheim, und Herrn Forstamtmann a. D. Marx, Rheurdt.

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BUCHBESPRECHUNGEN

MOSSMANN, H. W.: **Vertebrate Fetal Membranes.** Comparative Ontogeny and Morphology, Evolution, Phylogenetic Significance, Basic Functions, Research Opportunities. Basingstoke: McMillan Press, and New Brunswick, N. J.: Rutgers University Press 1987. 383 pp. £ 80.00; US $ 95.00. ISBN 0-8135-1132-1

Der Autor dieses Buches publizierte 1937 sein heute klassisches Werk „Comparative Morphogenesis of Fetal Membranes". Das neue Buch von MOSSMANN ist keine Neuauflage des früheren Werkes zum gleichen Thema, sondern ein völlig neues Buch. Der Inhalt ist wesentlich erweitert, da nunmehr alle Vertebraten einbezogen wurden und der umfangreiche Zuwachs an neuen Befunden, die in den vergangenen 50 Jahren erarbeitet wurden, nicht zuletzt durch die kontinuierliche Forschungsaktivität des Autors selbst, eingebaut wurde. Zahlreiche Lücken des Kenntnisstandes von 1937 konnten geschlossen werden, und Änderungen mancher theoretischer Deutungen wurden erforderlich.

Das Werk ist in erster Linie unter morphogenetischen und morphologischen Aspekten geschrieben und bietet eine zuverlässige und vollständige Informationsquelle zu Fragen der Frühentwicklung, einschließlich der extraembryonalen Anhangsorgane. Besonderer Nachdruck liegt auf der Lehre von der Placentation der Eutheria. Soweit irgend möglich, sind die physiologischen Grundprozesse berücksichtigt.

Die sehr umfassende vergleichende Bearbeitung bildet eine gute Ausgangsbasis zur Erörterung evolutiver und phylogenetischer Fragen. Da das intrauterine Milieu bei Säugetieren wesentlich geringere artliche Differenzen erwarten läßt, als der Komplex äußerer Faktoren, denen der Gesamtorganismus ausgesetzt ist, erkennt der Autor den Vorgängen der frühen Ontogenese einen hohen Erkenntniswert für stammesgeschichtliche Überlegungen zu. Grundsätzliche Überlegungen führen den Autor zur Neugliederung der Ontogeneseabläufe bei Wirbeltieren. Aufgrund der Beschaffenheit des Dottersackes und der Eistruktur unterscheidet MOSSMANN:

1. Sessilata: Dottersack erscheint als Ausweitung des Darmkanals, ungestielt und an der Bildung der Bauchwand beteiligt. Eier: meso-megalecithal (Cyclostomata, Chondrostei, Holostei, Dipnoi, Teleostei, Amphibia).
2. Pedunculata: Dottersack gestielt und kaum an Bildung der definitiven Bauchwand beteiligt (Chondrichthyes).
3. Amniota: Amnion, Chorion und Allantois, Dottersack definitiv ganz oder zum großen Teil trilaminär.
   a. Sclerostraca: Eier megalecithal mit Schale, Schalenhaut und „Albumen"-Schicht: Reptilia, Aves, Monotremata.
   b. Hymenostraca: Eier miolecithal. Schalenhaut, Albumen und Zona pellucida vorhanden: Marsupialia.
   c. Anostraca: Eier miolecithal, keine Schale und keine Schalenhaut. Selten eine dünne Albumenschicht vorhanden: Eutheria.

Das Werk enthält 77 Textabbildungen (Photos, EM-Photos, Diagramme) und 29 Tafeln, die jeweils in einer Anzahl von sorgfältig ausgeführten, schematischen Strichzeichnungen wesentliche Entwicklungsabläufe der verschiedenen Gruppen vergleichend darstellen. Das Buch kann nicht nur als zuverlässiges Handbuch und Nachschlagewerk dem Spezialisten wertvolle Dienste leisten, sondern ist wegen sehr klarer Sprache und didaktisch sorgsam überlegter Darstellungsweise auch hervorragend geeignet, jedem Biologen und Mediziner als Einführung zu dienen. Das Werk wird für lange Zeit seine grundlegende Bedeutung behalten und darf in keiner biologischen Bibliothek fehlen. Dem Autor gebührt Dank für diese Meisterleistung, dem Verlag für die ausgezeichnete technische Herstellung.

D. STARCK, Frankfurt/M.

BEGON, M.; MORTIMER, M.: **Population Ecology.** 2. Ed. Oxford: Blackwell Scientific Publications 1986. 180 pp., 200 ill. £ 10.50. ISBN 0-632-01443-1

Dieses Buch kann jenen empfohlen werden, die eine straffe und grundlegende Einführung in die Populationsökologie lesen möchten. Es wurden zoologische wie botanische Beispiele gleichermaßen berücksichtigt. Im Aufbau hat sich in der 2. Aufl. nichts wesentlich geändert. So werden auch jetzt die beiden Kapitel „Interspezifische Konkurrenz" und „Prädation" am umfassendsten behandelt. Sie spiegeln die englische Schule der Verhaltensökologie wider.

Das Buch kann für Studierende, die sich in die Populationsökologie einarbeiten wollen, sehr hilfreich sein.

R. SCHRÖPFER, Osnabrück

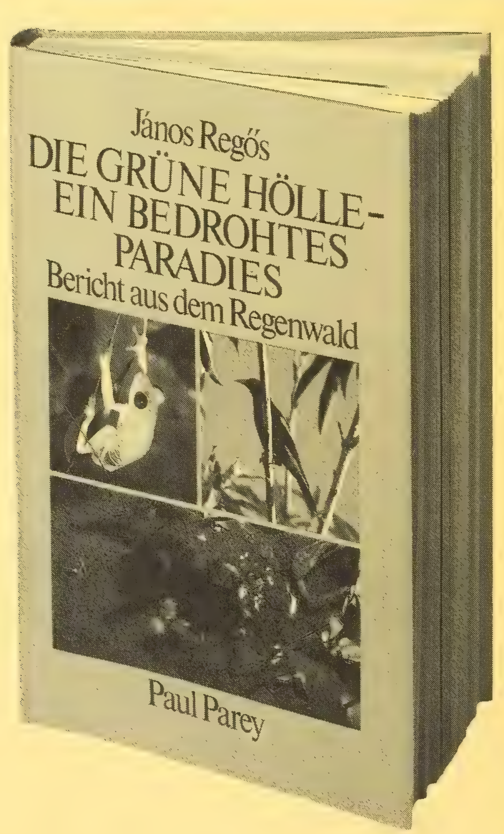
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Z. Säugetierkunde 53 (1988) 5, 257–320



János Regős
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PARADIES
Bericht aus dem Regenwald
Paul Parey

'ol. 53 (6), 321–384, Dezember 1988 ISSN 0044-3468 C 21274 F

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INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Organ der Deutschen Gesellschaft für Säugetierkunde



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Z. Säugetierkunde 53 (1988) 321–324

ISSN 0044-3468

Statut de trois espèces de chiroptères rares au Maroc: *Nycteris thebaica, Hipposideros caffer* et *Pipistrellus rueppelli*

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Réception du Ms. 15. 10. 1987

Abstract

Status of three rare bat species in Morocco: Nycteris thebaica, Hipposideros caffer and Pipistrellus rueppelli

Discussed is the occurrence of three rare species of bats in Morocco. *Nycteris thebaica* and *Hipposideros caffer* originate from Africa, south of the Sahara; in Morocco they live exclusively along the atlantic coast. *Pipistrellus rueppelli* which was caught in the presaharian area (Tafilalt) is reported for the first time in Morocco. The populations of all three species are considered as remnants.

Introduction

Au Maroc, les études mammologiques ont connu deux périodes d'intense activité: l'une au début du siècle dont les résultats sont rassemblés dans l'ouvrage de Cabrera (1932), l'autre dans les années cinquante avec les travaux de Panouse (1951, 1958, 1959) et de Brosset (1960). Mais les prospections d'alors se sont surtout limitées au Maroc septentrional alors que les régions situées au sud du Haut-Atlas restaient méconnues. Cette lacune tend à être comblée progressivement par les naturalistes résidents et par les visiteurs occasionnels, attirés par les paysages désertiques du Maroc présaharien. L'observation de trois espèces de chiroptères peu communs s'inscrit dans cette dynamique.

Matériel et méthode

Nos observations résultent essentiellement de la visite diurne des grottes karstiques et autres cavités souterraines; quelques captures directes ont été effectuées à cette occasion. Accessoirement, nous avons placé des filets de nylon sur des plans d'eau calme (flaques résiduelles d'oueds, bras de rivières, etc.) ainsi qu'à l'entrée d'un conduit de canalisation abandonnée.

Résultats

Nycteris thebaica Geoffroy, 1818 – Nyctère de la Thebaïde

Découverte assez récemment dans la proche région de Rabat (Panouse 1958), cette espèce d'origine éthiopienne semble répandue sur toute la façade atlantique marocaine. Trouvée peu de temps plus tard dans l'Anti-Atlas occidental (Panouse 1959), elle a aussi été collectée sur le versant septentrional du Haut-Atlas par la Smithsonian Institution, en 1971. La région d'Agadir héberge également, au moins temporairement, de petites colonies de *Nycteris:* l'une, forte d'une cinquantaine d'individus, fut découverte près d'Imouzzer des Ida Ou Tanane, en octobre 1985, dans une petite grotte (observation non renouvelée depuis en dépit d'un suivi régulier des cavités de la zone); l'autre, réduite à une dizaine

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d'individus, fut observée en avril 1986 et janvier 1987 dans une canalisation abandonnée près de l'embouchure de l'oued Massa.

Toutes les données relatives à cette espèce proviennent de cavités aux dimensions réduites; dans les deux derniers cas, la hauteur de la galerie n'excède pas un mètre. La température peut être très variable; oscillant entre 15 ° et 20 °C durant la période



Localités citées dans le texte: 1 = Tanger; 2 = Rabat; 3 = Essaouira et Mogador; 4 = Imouzzèr des Ida Ou Tanane; 5 = Agadir; 6 = Oukaïmeden; 7 = Foum Zguid; 8 = Aoufouss (Tafilalt); 9 = Abadla; 10 = Beni Abbès; a = oued Cherrat; b = oued Souss; c = oued Massa; d = oued Ziz. ◉ = stations de *Pipistrellus rueppelli* (quatre mentions pour l'Afrique du nord-ouest)

d'occupation (hiver) de la grotte de l'oued Cherrat (Panouse 1958), elle était de plus de 22 °C (automne) et largement supérieure à 26 °C (printemps) pour les dernières observations en date. Actives toute l'année, ces chauves-souris semblent se déplacer et changer de gîte fréquemment. Leur écologie demeure très floue (aucune colonie de parturition n'a été découverte à ce jour . . .).

Hipposideros caffer (Sundevall, 1846) – Rhinolophe de Cafrerie

Ce «Rhinolophe» est connu au Maroc depuis le début du siècle losque Cabrera (1906) décrivit l'espèce *Hipposideros tephrus,* sur la base d'un spécimen provenant de la région d'Essaouira. Les vues des taxonomistes divergent à cet égard, la plupart attribuent cependant à la population maghrébine le rang subspécifique adopté ici *(Hipposideros caffer thephrus).* Cabrera (1932) considère cette forme comme répandue «desde Tànger hacia el Sur (localidad tipica, Mogador), hasta el Senegal»; pourtant, aucune observation n'est venue actualiser ces données jusqu'à ces derniers temps.

La première découverte (étonnante!) fut celle d'un cadavre à l'Oukaïmeden (Haut-Atlas, 2500 m). Mais la confirmation de la présence de ce chiroptère au Maroc fut apportée par la capture, en avril 1985, de quatre mâles à l'entrée d'une canalisation abandonnée à l'embouchure de l'oued Massa. Ce gîte était réoccupé au printemps suivant par une colonie d'une vingtaine d'individus (un mâle capturé, avant-bras = 45 mm) et dans le courant de l'hiver par une quinzaine d'animaux très actifs.

Ainsi, à plus de cinquante ans d'intervalle, il est établi que la façade atlantique marocaine héberge cette espèce très répandue en Afrique au sud du Sahara.

Pipistrellus rueppelli (Fischer, 1829) – Pipistrelle de Rüppel

Le 19 avril 1985, parmi trois *Pipistrellus kuhli* (deux femelles et un mâle), une femelle de cette espèce était capturée au filet au-dessus d'un bras mort de l'oued Ziz, à Aoufouss (Tafilalt). Cette magnifique Pipistrelle se distingue d'emblée des autres représentants de son genre par la coloration de son pelage (poils du dos gris argentés, face inférieure blanc crème) et par la forme de ses incisives internes supérieures qui sont profondément bifides (Haymann et Hill 1971). La peau du visage et des oreilles est d'un brun très foncé, presque noire; les membranes alaires sont également gris-brun sombre. Les principales mensurations de cet animal sont les suivantes: avant-bras = 32.4 mm; 4ème doigt = 50.3 mm; 5ème doigt = 43.6 mm. Ce chiroptère est le seul représentant du sous-genre *Scotozous,* Dobson 1875, vivant sur le continent africain. La découverte de cette chauve-souris apporte un complément à l'étude des chiroptères de cette région qui est une zone de transition entre domaines paléarctique et saharien (Aulagnier et Destre 1985), mais aussi à la connaissance de la faune marocaine avec une vingt-sixième espèce de chauve-souris.

Après vérification, il s'avère que la Smithsonian Institution a également collecté un spécimen de *P. rueppelli* dans les environs de Foum Zguid, le 10 mars 1970 (femelle – 0470693), au cours de sa gigantesque campagne de prospection 1969–1972; cette observation est uniquement mentionnée dans le registre des collections de cet organisme. La capture filali constitue donc la seconde mention au Maroc pour cette espèce d'origine africaine qui paraît rare au nord du Sahara.

Discussion

Outre leur relative rareté, un trait commun à ces trois espèces est leur large répartition africaine qui les oppose aux autres chauves-souris qui peuplent le Maroc et qui sont paléarctiques pour la plupart, sahariennes pour les formes localisées dans les zones les plus méridionales. De fait, il s'avère que *Nycteris thebaica* et *Hipposideros caffer* fréquentent essentiellement la façade atlantique marocaine, en particulier la plaine du Souss, comme certains autres mammifères qui constituent des relictes de faune tropicale: *Crocidura viaria, Xerus erythropus, Mastomys erythroleucus Mellivora capensis,* etc.

La distribution de *Pipistrellus rueppelli* est sensiblement différente et plus complexe à interpréter: largement répandue en Afrique australe mais rare en Afrique de l'ouest, les données marocaines s'ajoutent à deux mentions algériennes (Beni Abbes [Haymann et Hill 1971] et Abadla [Gaisler et Kowalski 1986] – localités distantes repectivement de 250 et 150 km d'Aoufouss), établissant l'existence d'un peuplement sur la frange septentrionale du Sahara. Il reste à poursuivre les investigations pour préciser le statut de ces chauves-souris et ainsi appréhender les caractéristiques de leurs populations qui semblent relictuelles.

Remerciements

Nous remercions G. Dändliker, H. Duperrex, J. L. Rolandez, J. P. Marfin, L. Lesne et M. Thévenot qui ont participé aux recherches sur le terrain, le Professeur V. Aellen, Directeur du Muséum de Genève, qui a relu et critiqué le manuscrit, enfin A. Schubert, K. Zbinden et P. Zingg pour la traduction des résumés.

Résumé

Nycteris thebaica et *Hipposideros caffer* sont des chiroptères d'origine africaine, fréquents au sud du Sahara; au Maroc, ils n'ont été trouvés que le long de la côte atlantique. *Pipistrellus rueppelli,* capturé dans la zone présaharienne (Tafilalt), est mentionné pour la première fois au Maroc. Les populations de ces trois espèces peuvent être considérées comme relictuelles.

Zusammenfassung

Zum Vorkommen von drei seltenen Fledermausarten in Marokko: Nycteris thebaica, Hipposideros caffer und Pipistrellus rueppelli

Das Vorkommen von drei seltenen Fledermausarten in Marokko wird diskutiert. *Nycteris thebaica* und *Hipposideros caffer* stammen aus Afrika, südlich der Sahara. In Marokko leben sie ausschließlich entlang der atlantischen Küste. *Pipistrellus rueppelli* konnte im Südosten des Landes (Tafilalt) gefangen und damit zum erstenmal in Marokko nachgewiesen werden. Bei allen drei Fledermausarten dürfte es sich um Restpopulationen handeln.

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Z. Säugetierkunde 53 (1988) 325–332

ISSN 0044-3468

Occurrence and frequency of twin-fight in the Common marmoset *(Callithrix jacchus)*

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Receipt of Ms. 9. 6. 1987

Abstract

Studied frequency and occurrence of twin-fight in the common marmoset *(Callithrix jacchus)*. Twin-fight is found in 32 of 39 groups and in 27 of 83 litters. 39 twins are heterosexual, 23 isosexual female and 16 isosexual male. Twin-fights are most frequent in isosexual male (50 %) and female (46 %) litters, least frequent in male-female twins (17 %). The age of the combatants at twin-fight is on the average 188,5 days in mm-twins, 241,7 days in ff-twins and 237,1 days in mf-twins. Sibling competition is observed during the whole interbirth-interval of the α-female. Five twin-fights show a temporal relation to the first and second estrus post partum of the α-female. In 6 % of all twin-fights a combatant has to be removed in order to prevent severe injuries. Sibling competition is observed in groups of max. 10 members. A relatively high percentage of twin-fights (ca. 37 %) is noticed in very small groups and in absence of group members of the opposite sex (parents excluded).

Introduction

Agonistic interactions between infantile/juvenile social living mammals are the exception rather than the rule. The siblings of a given litter, for example Suidae, Canidae, Felidae or Cricetidae often quarrell for the access to the nipples of their mother or for food, and also during play sessions they may interact to some extent agonistically. However, all these interactions do not cause injuries to their familiar social partner (see also Sutcliffe and Poole 1984). Poor management conditions (e.g. overcrowding, stimulus deprived environment) often induces increased aggressiveness between littermates which may lead to severe physical consequences, and even to the death of one or the other sibling (e.g. cronism in piglets or hamsters).

All these dissociative interactions are characterized insofar as they are triggered by an actual event, for example the access to food or mother's nipples. Furthermore they do not seem to have negative longterm effects on the relationship of the combatants. On the contrary many authors have stressed the eminently associative character of the interactions between infantile mammals (for a survey see Fagen 1981).

In the behavioural ontogeny of the marmosets however, we can observe a process which does not seem to be promoted by an actual event – at least we could not detect it – which exclusively involves dissociative behaviours, and which often ends in severe physical, and possibly even psychic injuries in the 4–10 months old marmoset twins. This twin-fight (Sutcliffe 1980) or sibling competition (Kleiman 1979) is believed to determine the relative position of the twins in the hierarchy of the group.

According to Sutcliffe and Poole (1984) the twin-fight has longterm consequences on the hierarchical relationship of the siblings, that is, the dominance-subordination-relationship between the twins will not be altered as long as the twins live together in their

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Table 1. **Generation of twins and TF-frequency; TF – litter(s) with twin-fight; no TF – litters without twin-fight**

twin constellation		F_1	F_2	F_2^x	F_2/F_3	F_3/F_2	F_3	F_2^x/F_4	F_3/F_4	F_4/F_3	F_5F_4/F_3^x	$F_3^x/F_3^xF_5$	F_3F_5/F_3^x	Σ
mf	no TF	11	4	3		6	1	6	1					32
	TF		3				1	1	1	1				7
ff	no TF	5	3	1			1	3						13
	TF	2			1		2	2	1		1		1	10
mm	no TF	4	1+(1)	3		1								9+(1)
	TF	2	2−(1)				1		1			1		7−(1)
Σ	no TF	20	8+(1)	7		7	2	9	1					54+(1)
Σ	TF	4	5−(1)		1		4	3	3	1	1	1	1	24−(1)

( ) = twin-fight uncertain; x = generation of one parent unkown; handreared and fostered peers are excluded.

Table 2. **Relative and absolute frequencies of litters with and without TF**

twin constellation	no TF	TF	Σ	% TF
mf	32	7	39	18
mf (FM)	1		1	
mf (HR)	1		1	
Σmf	34	7	41	17
ff	13	10	23	44
mmff (HR)		1	1	
Σff	13	11	24	46
mm	9+(1)	7−(1)	16	44 (38)
m + m (FM)		1	1	
mm + mmf (HR)		1	1	
Σmm	9+(1)	9−(1)	18	50 (44)
Σ total	56+(1)	27−(1)	83	33 (31)

FM = peers reared by foster mother; HR = hand-reared; ( ) = TF uncertain.

natal group. KLEIMAN (1977) does not believe that marmoset families are hierarchically structured (compare however EPPLE 1975; ROTHE 1975, 1979; STEVENSON and POOLE 1976). On the other hand KLEIMAN (1979) refers to dominant and subordinate twins in *Leontopithecus rosalia rosalia*.

In the present paper we give data on the occurrence, frequency and the relationship of twin-fights to group size, sex ratio of the natal group, age at twin-fight, as well as the incidence of twin-fights during the interbirth-interval of the α-female.

Material and methods

83 litters (5 hand- and fostermother-reared peers included, see Table 2) of 32 families of our *Callithrix jacchus* colony could be analysed. In 39 litters the surviving siblings were bisexual, in 23 isosexual female and in 16 isosexual male. The size of the groups (parents and offspring) varied from 4 to 18 members. The generation of the twins/peers was F 1 to F 3F 5/F 3 (Table 1). The data were taken from the diary of our primate laboratory, in which we record all important biological and behavioural events which can be observed during the animals' daily activity (6–18 h).

The groups were housed in cages or rooms of 1.0 m × 2.0 m × 2.5 m to 5.0 m × 7.0 m ×3.0 m in size, each of them being equipped with free-swinging climbing frames, feeding boards and sleeping boxes. The animals usually could not see each other, however occasionally there was some acoustic and olfactory contact.

In addition to daylight artificial lighting was provided by neon tubes on a 12 hour cycle (6–18 h), and the rooms were screened by venetian blinds from 5.00 p.m. to 7.00 a.m. A constant temperature of 26 °C and a humidity of 70 % was maintained by means of an air conditioner. The animals were fed twice daily.

Most of the twin-fights (TF) were not observed directly, that is, we do not know the initiator and the special circumstances which triggered the sibling competition. From the numerous small wounds, which could be detected in the face and in other parts of the twins' bodies as well as from their aggressive interactions it was rather easy to infer, that TF had taken place. We cannot exclude, however, that we have overlooked one or the other TF, especially those which did not cause injuries or which were not accompanied by detectable aggressive interactions between the combatants.

Results

TF were noticed in 22 of the 32 groups (68.68 %) and in 27 of the 83 litters (32.5 %) (Table 2). In 3 groups we observed 2, in one group 3 TF (see also KLEIMAN 1979 for *Leontopithecus rosalia rosalia*).

Most frequent TF occurred in isosexual male litters (= mm-litters) (n = 9, 50.0 %). Isosexual female twins (= ff-litters) (n = 24) had also a high rate of TF (n = 11, 46 %), whereas male-female twins (mf-litters) (n = 41) had significantly lower TF-ratios (n = 7, 17 %). According to these data TF was observed in about one third of all litters. From these data we can conclude that TF is not a regular event in the ontogeny of the common marmoset infants/juveniles.

In 5 TF the loser was so severely attacked and injured by its sibling that he has to be removed from its family, one of them died 4 days following the TF (see also KLEIMAN 1979 for *Leontopithecus rosalia rosalia*).

In our *C. jacchus* colony TF was observed when the combatants were 4 to 10 months old. The maximum TF-age is rather identical in the three twin-constellations (see also SUTCLIFFE and POOLE 1984). The age of the combatants at TF was lowest in mm-twins (on the average 188.5 days, range 112–278 days). In ff-twins we find the highest TF-age (on the average 241.7 days, range 167–314 days), closely followed by mf-litters (on the average 237.1 days, range 209–314 days) (Table 3). The low TF-age of the mm-twins is mainly due to 2 TF which were observed when the combatants were only 4 months old.

As is demonstrated in the Figure TF are distributed over the whole interval between 2 births by the α-female of the group. The peak however lies in the first half (= 50–80 days)

Table 3. **Age of twins at twin-fight (in days)**

twin constellation	mean	range
mf	237.1	209–314
ff	241.7	167–314
mm	188.5	112–278

Table 4. **Relationship of mm-TF-frequency to sex ratio of the family; parents and following litter are excluded**

m/f	0	1	2	3	4	5	6	7	8	9	10
1											
2	TEX		E	(T)							
3	X	T	Ta	T							
4			T								X
5		X	Eb								
6			X	X							
7											
8			X								
9						2X					

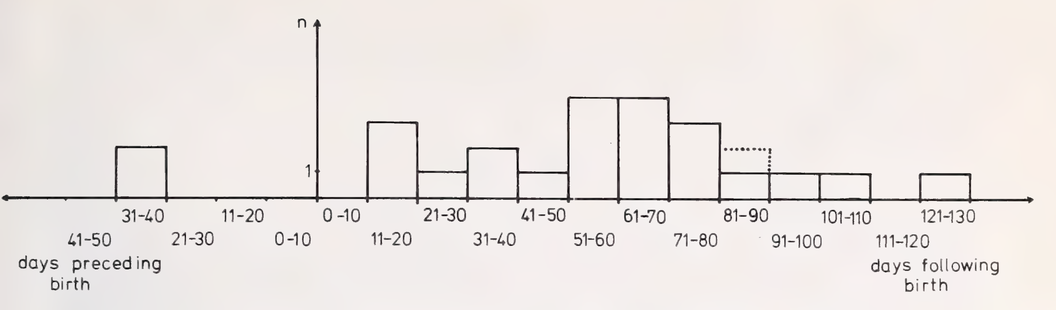
T = twin-fight; E = twin-fight related expulsion/removal; X = no twin-fight; ( ) = twin-fight uncertain; a = reared by foster mother; b = handreared

Table 5. **Relationship of ff-twin-fight-frequency to sex ratio of the family** (See legend of Table 4)

m/f	1	2	3	4	5	6	7	8	9	10	11
0		7TEX	2X	X							
1			TX	TX							
2											
3			Eb		X				X		X
4			2X			X					
5											
6											
7											
8					X						

Table 6. **Relationship of mf-twin-fight frequency to sex ratio of the family** See also legend of Table 4

m/f	0	1	2	3	4	5	6	7	8
0									
1		2T8X		3X		X			
2		2T	TX	Xa	2TX		X		
3		2X		X		X	X		
4		X		Xb			2X		
5					X	X		X	
6			X						
7									
8				X					X
9				X			X	X	



Incidence of TF in relation to preceding/following birth in the family group. n = frequency of TF; --- TF uncertain

of the α-female's pregnancy. The TF in the three twin-constellations are rather similar distributed over the interbirth-interval. Five TF however showed a temporal relation to the first and second estrus post partum of the α-female (days 11–37), the twins being 167 to 314 days old at that time.

TF which required the removal of a combatant occurred only in isosexual litters [n = 5; 3 twins, 2 handreared peers (male and female)]. If we exclude the handreared peers, then 12.5 % of all expulsions/removals of a group member followed a TF, and in only 6 % of all TF (n = 83) we had to remove a sibling in order to prevent severe injuries or even the death of the inferior twin.

Six from 9 TF of mm-twins and -peers were observed when the sex ratio of the group was in favour of males, 2 when the sex ratio was balanced, and only 1 when the females were in surplus. TF independent expulsions of group members could only be noticed when males were in surplus (see Table 4).

We obtain the same results for ff-siblings. Ten of 11 TF were seen when the sex ratio was in favour of females, only 1 when the group had a balanced sex ratio. Most of the TF were observed in groups with 6 to 10 members. It must be stressed however, that we did not see any TF in groups with extremely unbalanced sex ratio. Wether this depends on the unbalanced sex ratio or on the group size or on both, cannot be answered (see Table 5).

TF in mf-siblings could nearly exclusively be observed in groups with rather balanced sex ratio and with less than 10 group members (see Table 6).

In summing up we get the following results. In our *C. jacchus* colony we observed TF in groups of max. 10 group members. A relatively high percentage (approx. 37 %, n = 10, 8 in ff-twins) of TF was noticed in very small groups and in the absence of group members

Table 7. **Relationship of twin-fight frequency to sex ratio of the family**
Summary of Table 4–6

m/f	0	1	2	3	4	5	6	7	8	9	10	11
0			7TEX	2X	X							
1		2T8X		T4X	TX	X						
2	TEX	2T	TEX	TX	2TX		X					
3	X	T2X	T	TEX		2X	X			X		X
4		X	T	3X			3X				X	
5		X	E		X	X		X				
6			2X	X								
7												
8			X	X		X			X			
9				X		2X	X	X				

of the opposite sex (parents excluded). In that situation TF often led to the removal of a combatant. Between these two extreme situations it seems to give a stable group size with neither TF nor expulsions/removals (see Table 7).

Discussion

According to the data of our *C. jacchus* colony sibling competition is not a regular event in the relationship between young common marmosets. Even if we assume that many TF could not be observed, there still remained a large number of litters in which TF did not occur. The infants of wildcaught parents showed the least TF. With increasing number of generation the frequency of TF rises, but not continuously. It might be, however, that with increasing length of the existence of the colony in our laboratory a better monitoring of the animals was realized so that more TF could be detected compared to the first years of colony existence.

SUTCLIFFE and POOLE (1984) argue that TF have a longterm effect of the relative hierarchy between the combatants. We cannot confirm this view, since TF are not seldomly repeated and the rank position may be changed (see also KÖNIG, in prep.; KLEIMAN 1979 for *Leontopithecus rosalia rosalia*). TF-related expulsions are rather seldom. Since the age at TF is relatively low (see also SUTCLIFFE and POOLE 1984; KLEIMAN 1979 for *Leontopithecus* [10–12 months]; WOLTERS, pers. communication for *Saguinus oedipus oedipus* [8–12 months]), this means, that the animals are far from being adult (see ABBOTT and HEARN 1978) it seems biologically meaningful to prevent expulsions in order not to reduce too drastically life expectancy and/or reproductive success of the infantile/juvenile loser. According to SUTCLIFFE and POOLE (1984) TF must take place at an age when the permanent dentition has not yet developed to avoid dangerous injuries. In most TF which were noticed in our colony only minor wounds indeed occurred, but in some TF also severe injuries could be observed in both combatants (see also KLEIMAN 1979 for *Leontopithecus rosalia rosalia*). As yet we have no idea on the psychic effects/consequences of TF which might also be, even more important, than any physical wound.

Most remarkable is the sudden appearance – at least for the human observer – of TF. The initiating event was not observed in most cases. SUTCLIFFE and POOLE (1984) believe that the increase of intolerant behaviour of older group members towards the twins could stimulate the siblings to TF. KLEIMAN (1979) mentions as possible releaser for TF in *Leontopithecus rosalia rosalia* the first transfer of the youngest family members (= 2 weeks old) from the mother to the father. For both assumptions we do not have any indication from *C. jacchus*. Without further information on the initiating event it is somewhat difficult to understand that aggressiveness toward the twins should trigger more or less suddenly aggressiveness between them. We urgently need more data on this aspect.

According to ABBOTT (1978) *C. jacchus* already show from the sixth month of age considerable changes in the estradiol (female) and testosterone (male) levels. These data fit relatively well to the TF-age. Therefore it might not be unrealistic to assume that the endocrine status of the twins could influence, and may be the primary cause for TF. If this is the case then TF would be a regular event in the development of common marmosets and we had overlooked a considerable number of TF in our colony. It may be, however, that many TF proceed less spectacularly, i.e. in a strong ritualized, non-fighting manner, so that they are hardly to detect.

Our data show that TF are influenced by the size and the sex ratio of the family. It is most striking, that TF very often occur in small groups, that is in groups in which besides the parents no other or only very few adult members live. According to our observations these groups are only scarcely hierarchically structured. The probability to collide with an adult brother or sister is essentially lower in small than in large groups in which TF

typically occur seldom or not at all. This result does not fit to SUTCLIFFE and POOLES (1984) hypothesis on the initiating event/animal of TF.

At least some TF seem to be triggered by the estrus of the α-female, especially by the post-conception-estrus in mid-pregnancy. KLEIMAN (1979) also observed in *Leontopithecus rosalia rosalia* estrus related TF and parent-offspring-conflicts during mid-pregnancy (mid-pregnancy false estrus sensu KLEIMAN and MACK 1977).

As a whole there exists only a small bulk of data on TF in Callitrichidae and no information on the question whether we are right in assuming that siblings are even-ranking up to TF. ENGEL (1986) has shown that twins already reveal remarkable differences as to their social competence in early infancy. We do not know as yet however which event(s) or process(es) may be responsible for these differences in the relative position of the twins in the group hierarchy. This would mean that TF must have other and/or different function(s) as was hitherto believed. Up to now the published data on TF in marmosets and tamarins are too small for a sufficient explanation of the functional aspect of this behavioural phenomenon.

Acknowledgements

We are greatly indebted to Miss T. GATESMAN for her help in translating this article into English.

Zusammenfassung

Auftreten und Häufigkeit von Zwillingskämpfen beim Weißbüscheläffchen (Callithrix jacchus)

Zwillingskampf wurde in 32 von 39 Gruppen und in 27 von 83 Würfen des Weißbüscheläffchens *Callithrix jacchus* beobachtet. 39 Würfe waren heterosexuell, 23 isosexuell weiblich und 16 isosexuell männlich. Am häufigsten waren Zwillingskämpfe in reinen Männchen- (50 %) und isosexuellen Weibchenwürfen (46 %), am seltensten (17 %) unter heterosexuellen Wurfgeschwistern. Das Zwillingskampf-Alter betrug bei männlichen Wurfgeschwistern im Durchschnitt 188.5 Tage, bei weiblichen 241.7 Tage und bei heterosexuellen 237.1 Tage. Zwillingskämpfe waren über den gesamten Intergeburtenabstand des α-Weibchens verteilt, fünf zeigten eine zeitliche Beziehung zum 1. bzw. 2. postpartum-Östrus der Mutter. In 6 % aller Zwillingskämpfe mußte ein beteiligtes Tier aus der Gruppe entfernt werden, um schwere Verletzungen zu vermeiden.

Zwillingskämpfe konnten nur in Gruppen mit max. zehn Mitgliedern beobachtet werden, wobei ein relativ hoher Prozentsatz (37 %) in sehr kleinen Gruppen und in Abwesenheit gegengeschlechtlicher Gruppenmitglieder (Eltern ausgenommen) zu verzeichnen war.

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Z. Säugetierkunde 53 (1988) 333–340

ISSN 0044-3468

Homing behavior of Wood mice *(Apodemus)* in a geomagnetic anomaly

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Receipt of Ms. 1. 6. 1987

Abstract

Experiments have been performed to test the hypothesis that a previously described local directional bias in the homing behavior of wild mice resulted from an interference between homeward orientation and a tendency to go up the gradient of magnetic intensity at the site of a weak geomagnetic anomaly. An analysis of homing success of 440 European woodmice (*Apodemus flavicollis* and *A. sylvaticus*) tested at any of four sites affected by the same magnetic anomaly provides only limited support to the hypothesis. The results point to the possibility that a stronger effect of the anomaly could be a drop in homing success in the immediate surroundings of the magnetic trough of the anomaly.

Introduction

In the early 1960's, one of us carried out a homing experiment near Lausanne, Switzerland, with European wood mice (*Apodemus sylvaticus* and *A. flavicollis*), in which animals displaced from different cardinal directions had different homing performances (Bovet 1962). Using the terminology of the time, he described the differential pattern as a directional effect (= Richtungseffekt) (e.g. Kramer et al. 1956, 1958; Pratt and Wallraff 1958). Subsequently, we learned from a paper by Meyer de Stadelhofen et al. (1973) that Bovet's (1962) research area was located in the Jorat magnetic anomaly (see Fig. 1,A). In the mean time, evidence had been accumulating on the role of magnetic cues in bird orientation (reviewed by Keeton 1974). This led us to perform, in 1975–1977, the series of experiments reported in this paper to evaluate the possibility that the directional effect described by Bovet (1962) was linked to the magnetic anomaly, and that natural magnetic cues could affect the orientation of mice. The results obtained were not clearly interpretable in terms of a magnetic effect at this time and were filed away.

Since then, experiments with pigeons have led to a better characterization of how and when their homing orientation and/or performance is affected after release in various kinds of magnetic anomalies (review in Wagner 1983). On the other hand, several experiments have been performed with rodents, some of which suggest an important role of magnetic cues in the homing orientation of these animals (Mather and Baker 1981; August 1985), others not (Etienne et al. 1985, 1986). These recent developments on the role of magnetic cues in the spatial orientation of higher vertebrates prompted the present re-examination of the results of the 1975–1977 experiments.

The Jorat magnetic anomaly, a part of which is shown in Fig. 1, comprises a fairly uniform disruption of the normal pattern of gradients of total magnetic field intensity, that affects an area of roughly 50 × 35 km (Meyer de Stadelhofen et al. 1973). Bovet's (1962) major basis for assuming a directional effect was that in the area he worked in (around A in Fig. 1), the homing success (= ratio of number of successful homers to number of animals tested) was highest for animals which had to travel up to 1 km South in order to home, null for animals which had to travel toward North, and intermediate

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Fig. 1. Map of the Jorat magnetic anomaly. Numbers on isodynamic lines indicate total magnetic intensity at ground level (in nT, +46 000). A, B, C, D are the central points of the four experimental areas. R is point 530,000/160,000 of the Swiss reference grid system. Stripped area is part of Lake of Geneva. (Redrawn from Meyer de Stadelhofen et al. 1973, with permission)

toward East and West, with slightly higher figures toward East than West (Fig. 2). Considering that the magnetic isopleths in the area around A run along an ENE-WSW axis and the gradient goes up toward SSE (Fig. 1), we hypothesized that, in addition to a homeward tendency, the mice may have a tendency to go up the abnormally steep magnetic gradient (i.e., about 70 nT/km vs. about 10 nT/km in normal conditions, at ground level). The convergence of the two tendencies should facilitate homing, whereas their divergence should impair it. This would account not only for the strong difference between South and North and the intermediate values for East and West, but also for the small difference between East and West: animals homing toward East go slightly up the gradient; animals homing toward West go slightly down the gradient. Our 1975–1977 experiments were then aimed at testing the following predictions of the hypothesis with respect to homing success:

1. New displacements performed in the area around A should reveal the same directional effect as in 1962.
2. Displacements performed in an area such as that around B (Fig. 1), where the magnetic isopleths have the same orientation and the gradient goes up in the same direction as in the area around A, should reveal the same directional effect.
3. Displacements performed in an area such as that around C (Fig. 1) where the magnetic isopleths are oriented NNE-SSW and the gradient goes up toward WNW, should reveal a directional difference such that homing success toward West is high, toward East low, and toward North and South intermediate with a small advantage for North.
4. Displacements performed in an area like that around D (Fig. 1), which is in a magnetic trough, should not reveal any directional difference.

The hypothesis and its predictions were based on the 1962 experiment and on the description of the anomaly by Meyer de Stadelhofen et al. (1973), with no specific input from other sources. However, during the tests, they received support from a paper by Frei and Wagner (1976). These authors reported then that homing pigeons released at various sites within the very same Jorat magnetic anomaly had an initial orientation which was a

compromise between homeward orientation and a tendency to fly up the magnetic gradient, thus something very similar to our hypothesis. On the other hand, the evidence eventually produced by MATHER (1985) suggests that the magnetic deposits found in the head of woodmice make them potentially as sensitive to magnetic cues as, for instance, pigeons. According to GOULD (1982), behavioral evidence suggests this sensitivity to be at least 10–30 nT in pigeons; also, the single domains of magnetite discovered in pigeons could produce a resolution better than 1 nT. Taken together, these data suggest that, along the steepest slope of the gradient in the Jorat magnetic anomaly, woodmice could detect differences in field strength over distances of the order of 200 m or less. Our hypothesis was, therefore, not unreasonable in this respect.

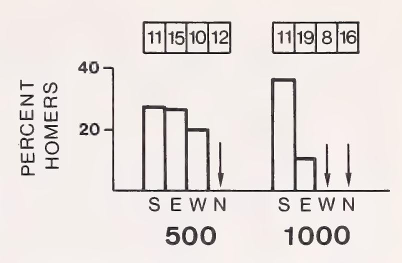


Fig. 2. Results of the 1962 experiment: homing success obtained at various stations around release site A (see Fig. 1), in percent of animals that homed. Numbers in boxes indicate numbers of animals displaced. S, E, W, N correspond to direction of home site, as seen from A. 500 and 1000 are distances (in m) from release site to home site. Vertical arrows point to zero values. Difference in homing success between South and North was nearly significant at 500 m, and significant at 1000 m ($p = 0.094$ and $p = 0.019$, respectively; Fisher's exact probability test, one-tailed). Concordance between the two distance conditions for a decrease of homing success figures in the order S-E-W-N was nearly significant: Spearman's $r_s = 0.95$)

Material and methods

The experiments were performed in four areas centered around points A, B, C, and D shown on Fig. 1. Grid references according to Carte nationale de la Suisse (1:25 000) are: A = 543,900/159,800; B = 544,850/160,280; C = 554,600/157,300; D = 544,800/165,500. The point of lowest magnetic intensity recorded by MEYER DE STADELHOFEN et al. (1973) within the contour of the 46 250 nT isopleth is located 1200 m ESE of D (their station 172: 46 238 nT).

In each area, a number of trapping stations were established according to a symmetrical pattern around the central point. Each station had 20 home-made single catch live-traps, on 4 rows of 5 traps forming a grid of 10 × 10 m squares. We tried to find areas as large as possible that would be at an appropriate location with respect to geomagnetic characteristics, and would cover homogeneous habitat. It is extremely difficult to find large areas of homogeneous habitat in a densely populated country like Switzerland, and we had to content ourselves with areas that were essentially "wooded" (with a variety of deciduous and coniferous species), with no major clearings. Around A and B, we could place 12 stations each, at 250, 500, and 750 m North, East, South and West of the central point. Around C, we could place only 8 stations, at 250 and 500 m North, East, South, and West of the central point. Around D, we were limited to 6 stations at 250, 500 and 750 m South and North of the central point. In any one area, all the stations were operated similarly and simultaneously. Details on trapping operations are shown in the Table. All the traps were checked every morning after a night of operation.

All the mice were marked at first capture with numbered ear-tags and with toe-clips. Only mice considered as residents of a home range overlapping a single trapping station were used in the experiments. Criteria for residency were that a mouse should have been captured at least three times on at least five consecutive calendar days, and should have been always captured at the same station. All the mice used in a given area were displaced and released at the central point of that area, at places marked A, B, C, and D in Fig. 1. Displacements were performed by transporting the mice on foot and by car in individual jars without view of the surroundings. Routes followed during displacement resulted from a compromise between avoiding long detours for the mice and allowing the trapper(s) to complete trap checking between sunrise and noon at the latest. All displacements were followed by release on the same day.

Depending on when a given mouse was displaced, traps were available for recapture at the home station a variable number of nights. For the last displaced mouse in any area, traps were available for at least 5 nights after release, spread over at least 7 calendar days. There was no obvious natural barrier between any home site and the corresponding release site. All the occasional rivulets and creeks were of a type passable by mice (BOVET 1965). The only two-lane paved road that went between several home sites and release sites (in areas A and B) was of a type passable by mice (KOZEL and FLEHARTY 1979) and was actually crossed by several successful homers (which could not have homed without doing so).

Trapping schedules. (Dates formated D.M.Y.)

Area	Number of stations	Begin of trapping	First displacement	Last displacement	End of trapping	Number of nights of trapping	Number of mice displaced
A	12	16. 10. 75	22. 10. 75	7. 11. 75	21. 11. 75	22	93
B	12	9. 8. 75	14. 8. 75	3. 10. 75	11. 10. 75	42	151
C	8	6. 4. 76	21. 4. 76	11. 6. 76	19. 6. 76	49	141[a]
C	8	12. 8. 77	25. 8. 77	6. 10. 77	13. 10. 77	43	
D	6	25. 10. 77	3. 11. 77	10. 11. 77	25. 11. 77	18	55

[a] 1976 and 1977 pooled for area C.

The experiments involved 440 *Apodemus*, each used only once. Numbers of mice studied in any one area are shown in the Table. Of these, 245 (145 ♂♂ and 100 ♀♀) were identified as *A. flavicollis*, and 174 (98 ♂♂ and 76 ♀♀) as *A. sylvaticus*. The remaining 21 mice (10 ♂♂ and 11 ♀♀) could not be attributed safely to either species, due to "intermediate" field identification characters. For the analysis of results, all 440 mice were pooled, irrespective of the species they belonged to. According to Mermod (1969), home range sizes are similar in the two species, which, as a rule, implies similar homing performances (see Anderson et al. 1977; Bovet 1978).

Source for statistical tests was Siegel (1956).

Results

Homing success values obtained at any one trapping station are shown in Fig. 3. Due to the well known depressing effect that displacement distance has on homing success (Bovet 1978), comparisons related to our magnetic hypothesis can be meaningfully made only

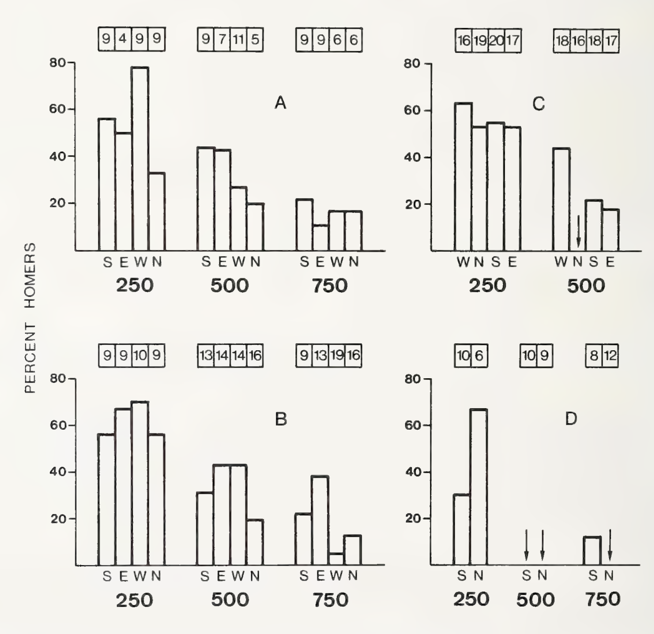


Fig. 3. Homing success obtained at the various stations in areas A, B, C, and D, in percent of animals that homed. Numbers in boxes indicate numbers of animals displaced. S, E, W, N correspond to direction of home site, as seen from release site. 250, 500, 750 are distances (in m) from release site to home site. Vertical arrows point to zero values

among stations that are at the same distance from the release site. An analysis of the relationships between homing success and distance in areas A and B has been published elsewhere (Bovet 1982).

Areas around A, B, or C

For each displacement distance in any area around A, B, or C, the four histogram columns displayed in Fig. 3 are arranged in descending order based on the predictions of the hypothesis. Of the 48 possible comparisons between any two values obtained in the same area and over the same distance, only three reveal a significant difference at the 0.05 level (χ^2 or Fisher's exact probability test, one-tailed): area B, 750 m, E>W; area C, 500 m, W>N, and W>E. If, in an attempt to overcome the effect of small sample sizes, we pool the comparable values obtained around A, B, and C (i.e., all results obtained over a given distance in directions corresponding to expected highest, second highest, third highest or lowest levels, respectively), the statistical results remain essentially the same. A significant difference is found in only two cases out of 18: 500 m, expected highest > expected lowest; and 750 m, expected second highest > expected third highest. It is thus obvious that, at this level of analysis, the statistics do not confirm the predictions of the hypothesis. There is however a trend, apparent in Fig. 3, for homing success to be higher in those circumstances where the hypothesis predicts it to be higher. Considering values that correspond to expected highest and lowest levels in any set of comparable figures (S vs. N around A or B, W vs. E around C), a sign-test shows the former to be significantly more often the highest of the two than expected by chance ($N = 7$; $x = 0$; $p = 0.008$). If we give up the rather stringent prediction of a consistent difference between expected second and third highest levels and we pool these two into a single "intermediate" level, there is a significant concordance among the experimental conditions for a decrease of homing success from expected highest through intermediate to lowest levels (Kendall coefficient of concordance; $N = 3$, $k = 8$, $s = 51.5$; $p < 0.05$).

Area around D

There is no significant difference in homing success between South and North over the three distances tested. Although this fits the prediction of the hypothesis, it has no real supporting value because the similar analysis applied to the other areas does not verify the contrasting predictions. Not predicted by the hypothesis, homing success over any one distance was steadily lower around D than around either A, B, or C (all directions pooled). The differences were particularly strong over 500 m (D<A: $p < 0.01$; D<B: $p < 0.01$; D<C: $p < 0.05$). This difference between area D and the other areas cannot be related to any obvious topographical or vegetational feature, nor to a matter of time of year when the experiments were carried out (compare A and D, Table).

Discussion

The results of this study provide limited support of the hypothesis that the homing performance of *Apodemus* was facilitated in certain directions and impaired in others as an effect of the magnetic anomaly. We did find evidence for a pattern of directional differences in homing success that coarsely fits the predictions of the hypothesis, but these differences were of very low amplitude and affected the overall homing performance in a marginal way only. On the other hand, the results indicate that the absence of a directional gradient of magnetic intensity in the trough of the anomaly (around D) might impede homing performance in mice.

The marginal effect of the anomaly on the homing performance in areas A, B, and C

seems to contradict the claims of MATHER and BAKER (1981) or AUGUST (1985) to the effect that woodmice *(Apodemus sylvaticus)* or white-footed mice *(Peromyscus leucopus)* are strongly disoriented after displacement in a disturbed magnetic field. The contradiction is apparent only. In MATHER and BAKER's (1981) as well as in AUGUST's (1985) experiments, the magnetic field was altered only during displacement, and returned to normal before release. By contrast, in our experiments, the "alteration" of the field was steady during both displacement and homing trip, a condition that did not affect the homing performance of hamsters in an arena (ETIENNE et al. 1985, 1986). Also, due to the size of the Jorat anomaly, it can safely be assumed that all our mice had spent their whole life within it. Considering current models of the ontogenetic development of navigational abilities in free-ranging animals (e.g., WILTSCHKO and WILTSCHKO 1982; BAKER 1984), it can be argued that the features of the magnetic anomaly were normal indeed to our mice and that the animals were tested in an "undisturbed" magnetic field. Furthermore, the magnetic changes produced experimentally by MATHER and BAKER (1981) and by AUGUST (1985) were claimed to act directly on the homeward orientation process of the mice, while the limited effect documented in this study seems to result from the interference of a tendency to go up a magnetic gradient with an otherwise normal homeward orientation process. This part of our results, therefore, pertains to MATHER and BAKER's (1981) or to AUGUST's (1985) findings only in as far as it suggests, however elusively, that magnetic cues can affect spatial orientation in wild mice. For the rest, it neither supports nor infirms these authors' conclusions. Similarly, and for the same reasons, our results provide no other element in the argument developed in recent years as to whether or not humans use magnetic cues for their homeward orientation (BAKER 1981; GOULD and ABLE 1981; FIDLES et al. 1984; WESTBY and PARTRIDGE 1986). On the other hand, the overall low homing performance that we observed in the magnetic trough is more consistent with the conclusions of MATHER and BAKER (1981) and of AUGUST (1985) that mice use magnetic cues as a basis for route-based navigation. However, several replications of the observation should be made before the possibility can be excluded that the effect was due to non-magnetic, local factors.

During the last decade, several experiments have been performed on the homing behavior of pigeons released in geomagnetic anomalies (e.g. FREI and WAGNER 1976; WAGNER 1976; WALCOTT 1978; FREI 1982; KIEPENHEUER 1982; LEDNOR and WALCOTT 1983; for a review, see WAGNER 1983). Besides the species used, there are a number of basic differences between these experiments and those reported in the present paper. Most pigeons experiments were performed in "strong" anomalies the geophysical effects of which are more intense than in the Jorat anomaly at ground level, but extend over a much smaller area, and result in a chaotic local pattern of magnetic intensities. They were usually performed with "experienced" animals, thus likely to use location-based systems of orientation, by contrast to our fully "naive" mice, that were more likely to use route-based systems (see WILTSCHKO and WILTSCHKO 1982; BAKER 1984). Finally, they involved the displacement of pigeons from outside the anomaly into it. Because of these fundamental differences in procedures, any attempt to compare the results of these studies with ours appears to be pointless. However, some of the experiments reported by FREI and WAGNER (1976) are much more related to ours. Besides being performed in the same, weak magnetic anomaly, they involved pigeons that were little trained and/or that had both their home site and their release site in the anomaly. As mentionned in the introduction, FREI and WAGNER's (1976) results suggest an effect essentially similar to our effect, i.e., a compromise between homeward orientation and a tendency to move up the magnetic gradient. The effect in pigeons, measured on the distribution of individual bearings at various times between release and vanishing, was more pronounced close to the release site (presumably a few hundred meters, i.e., the range on which we measured it in mice) than farther away (up to 3 km). Eventually, FREI (1982) reported on additional experiments in the same

anomaly. Releases made at places magnetically similar to our sites A, B, and C (his places 2 and 4) produced the same effect (FREI 1982, p. 136). But it should be pointed out that, in his 1982 paper, FREI argues that the general tendency to fly up the gradient in his experiments represents a particular case of a strategy which would induce a tendency to fly down the gradient when the field intensity at the home site is lower than at the release site (as in WAGNER's, 1976, experiments in the Chasseral anomaly, for instance). Applied to our mice, FREI's (1982) argument would imply that mice displaced from North to South in areas A and B, and from East to West in Area C should have their homing facilitated by a tendency to run down the gradient, which was apparently not the case. However, FREI's (1982) presentation of results is limited to vanishing bearings (at up to 3 km from release site) and does not differentiate among pigeons according to level of previous training and experience, which makes comparisons with our results more difficult.

Acknowledgements

This research was supported jointly by Natural Science and Engineering Research Council of Canada (grants A-6639 and T-0743 to J.B.) and by the Swiss National Science Foundation (grant 2.886-1.72 to M. D. and F. SCHENK). We are grateful to Drs. J. J. DODSON, A. ETIENNE, U. FREI and R. H. TAMARIN for critical reading of the manuscript; and to Drs. C. MEYER DE STADELHOFEN and F. MOREL and to the Société vaudoise des Sciences naturelles for counselling in geophysical matters and/ or for permission to publish Fig. 1.

Zusammenfassung

Heimfindeverhalten von Wald- und Gelbhalsmäusen (Apodemus) in einer geomagnetischen Anomalie

Die Hypothese, daß ein vorherbeschriebener „Richtungseffekt" im Heimfindeverhalten von wilden Mäusen durch eine lokale Störung des Erdmagnetfeldes verursacht war, wurde in einem Freilandexperiment geprüft. Der Heimkehrerfolg von insgesamt 440 an vier verschiedenen Stellen des magnetischgestörten Gebietes verfrachteten *Apodemus* stützt die Hypothese nur schwach. Die Ergebnisse zeigen nur nahe der Mitte zwischen den Orten größter magnetischer Intensität einen möglicherweise hemmenden Effekt auf den Heimkehrerfolg.

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Z. Säugetierkunde 53 (1988) 341–348

ISSN 0044-3468

Activity pattern and thermoregulation in the Cuis (*Galea musteloides* Meyen, 1833)

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Receipt of Ms. 29. 6. 1987

Abstract

Studied basal energetics, thermoregulatory reactions and nycthemeral variation of activity in seven cuis *(Galea musteloides)*. In female animals mean T_{re} was at the same level during day and night (37.3 and 37.4 °C, rsp.). In the males a marked peak was obvious around the transition from L- to D-phase. When exposed to temperatures from 15–35 °C T_{re} was regulated between 36.5–38.5 °C. Exposure to temperatures above 35 °C led to a rapid rise of T_{re}. O_2-consumption was lowest between 30–35 °C; however, BMR in the females was much lower than in the males (0.69 vs 0.94 ml/g·h). This is 17 % below (females) and 15 % above (males) the expected mass-specific value. The increase of O_2-uptake at ambient temperatures below the TNZ was also markedly less in the females. The slope of the regression line was 30 % (females) and 12 % (males) below the calculated mass-specific value for thermal conductance. Measurements of skin temperatures at various parts of the body revealed that in a cold environment heat flow to the periphery was mainly reduced at the tip of the nose and the hind foot pad. Under normal caging conditions activity patterns differed markedly between the sexes: Whereas in the males activity was uniformly distributed over D- and L-phase the females were about twice as active during the night. Additionally, in the female sex a stronger tendency towards longer lasting activity bursts was found.

Introduction

Cuis (vernacular name: pampahuanca) belong to the family Caviidae. The genus *Galea* contains three species which live in two geographically isolated areas (Cabrera 1961; Hückinghaus 1961): *G. musteloides* has its distribution area in Bolivia and the north-west of Argentina (from 600 to about 4000 m above sealevel) whereas the other two species occur only in the north-eastern parts of Brazil. Although this distribution area belongs to the tropical and subtropical zone, the climatic conditions can be described as temperate. Highest ambient temperatures occur during January with maximal values around 30 °C and lowest temperatures are found during July with the minimum near 0 °C. The area receives rather little rainfall, the bulk of it falling during the hottest month (January).

Although breeding colonies of cuis have been established in a number of laboratories and zoos during the last decade, information about this species is still rather scarce. Investigations have mainly concentrated on sexual and social behaviour (Weir 1971; Tam 1972; Rood 1972; Rowlands and Weir 1974). Nothing, however, is known about physiological parameters. As cuis quickly become tame and breed well in captivity they would appear to make an excellent laboratory animal (Rood 1972). It was the aim of this study, therefore, to obtain some basic values of the energetics and thermal demands of this species. Additionally, the nycthemeral rhythm of activity was investigated.

Material and methods

Seven cuis were used in this study. Two couples (all about one year old) were purchased from the zoos of Zürich and Stuttgart; they gave birth to three young ones in our laboratory. Mean body mass was 330 g in the females and 314.5 g in the males. The cuis were kept as pairs in wooden cages (73 × 73 ×

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50 cm) at room temperature 22 ± 1 °C, relative humidity 50 ± 5 % and at a L:D-cycle of 12:12 hours. Food consisted of a mixture of sunflower seeds, rolled oats, barley, commercial pellets, yeast powder and minerals. Additionally lettuce, apples and carrots were offered as well as grass, clover and dandelions if available. Occasionally biscuits and crispbread were added. Fresh water was always available.

Rectal temperature (T_{re}) was measured at a depth of 2.5 cm with a thermistor (Ultrakust, Thermophil; accuracy ± 0.1 °C). To obtain the nycthemeral variation of T_{re} under normal caging conditions not more than four measurements were made during any one day. O_2-consumption and CO_2-production were recorded in an open flow system using analyzers from HARTMANN and BRAUN (Oxytest, Uras). For the measurements the animals were placed in a perspex cylinder (∅ 18.7 cm, length 20 cm). Exposure to the various ambient temperatures (T_a) took place in a temperature controlled cabinet (Ehret) where T_a could be regulated to ± 0.5 °C. Air flow was adjusted to 34.8 l/h (T_a 20–35 °C) and 60.9–69.6 l/h (T_a 15, 37 and 40 °C), respectively. Constancy of air flow was continuously controlled by means of a flowmeter (ROTA). All gas volumes have been corrected to STPD.

Measurements of gaseous exchange were conducted during the second half of the D-phase because T_{re} of the males was lowest during this period. Exposure to the various ambient temperatures lasted for 5 h. At T_a > 35 °C, however, the experiments were disrupted earlier when the animals became restless. Calculation of gaseous exchange started only after an equilibration time of two hours the reported values representing the means over the following period of ca. 3 h. Immediately after opening the respiration chamber T_{re} and body mass were measured.

Skin temperatures (T_s) were obtained with a special surface temperature probe (United Systems Corp., model 581C, 709A). During these experiments the cuis remained in their normal cages and T_a in the room was set to 15, 22 and 34 °C, respectively. Skin temperatures were measured 3 and 7.5 h after changing T_a.

To find out about the nycthemeral variation of locomotor activity the cuis were watched using an infra-red sensitive video-camera (Grundig). Each of the adult couples was observed twice over a complete 24 h period. Length of active and resting periods was registered and occurrence of certain activities noted (e.g. feeding, drinking, grooming, sand-bathing, defecating).

Results

Nycthemeral variations of T_{re}

In the females no obvious diurnal rhythm of T_{re} could be detected (Fig. 1). Mean T_{re} during L-phase and D-phase were nearly identical: 37.3 ± 0.2 °C vs 37.4 ± 0.2 °C. A similar situation was found in the males; however, in this sex a marked peak occurred around the time when the lights were switched off in the animal room. Mean T_{re} then was at 38.4 ± 0.2 °C but dropped to 37.3 ± 0.2 °C within the next 2 h.

T_{re} after exposure to various ambient temperatures

In both sexes T_{re} was regulated within the normothermic range (36.5–38.5 °C) at ambient temperatures from 15–35 °C (Fig. 2). Exposure to higher T_a led to a rapid rise of T_{re} (to above 41 °C after 50–75 min at T_a 40 °C). Experiments then usually had to be disrupted because the cuis showed signs of severe heat stress (restlessness, defecation, urination).

O_2-consumption at T_a from 15–40 °C

In the females oxygen consumption was markedly lower than in the males over the whole range of tested ambient temperatures (Fig. 3). In both sexes minimal O_2-uptake occurred at T_a from 30–35 °C. Within this thermoneutral zone (TNZ) the basal metabolic rate (BMR) of the females was 17 % below and that of the males 15 % above the mass-specific value as expected after the formula of KLEIBER (1961).

At T_a below 30 °C O_2-consumption increased linearly in the females whereas in the males it showed a more irregular pattern. The increase can be described by the following regression equations:

females: $Y(ml\ O_2/g \cdot h) = 1.795 - 0.038 \cdot T_a\ (°C)\ (r = -0.91)$

males: $Y(ml\ O_2/g \cdot h) = 2.493 - 0.049 \cdot T_a\ (°C)\ (r = -0.73)$

The slope of the regression lines is 30 % (females) and 12 % (males), respectively, below the calculated mass-specific values after the formula of HERREID and KESSEL (1967). With the exception of T_a = 15 °C mean values of females and males are significantly different ($p \leq 0.05$).

At ambient temperatures above the TNZ O_2-consumption increased only moderately.

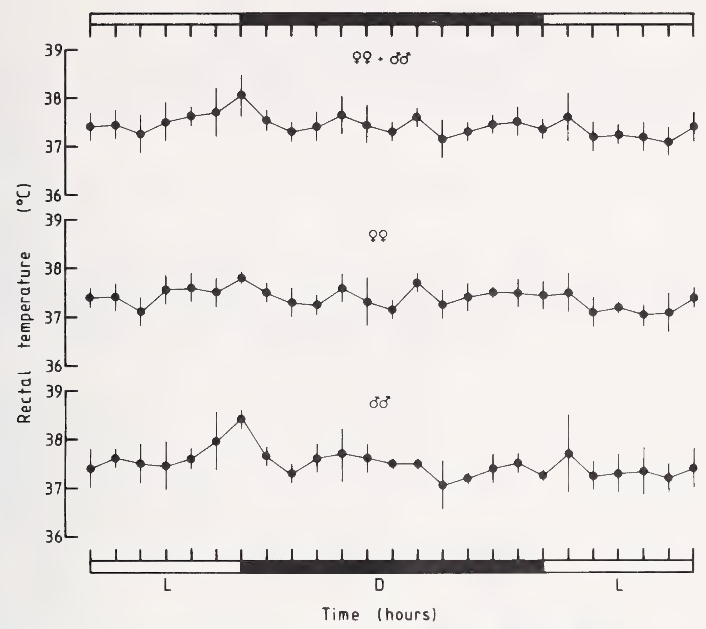


Fig. 1. Nycthemeral variation of rectal temperature (mean values ± S.D.) in cuis (3 males, 4 females). Each animal was measured twice at every full hour

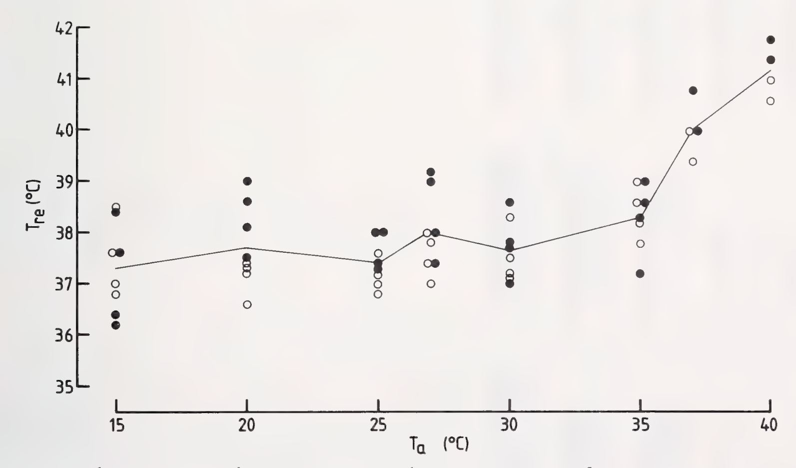


Fig. 2. Rectal temperature after exposure to ambient temperatures from 15–40 °C. Exposure lasted for five hours except for ambient temperatures above 35 °C when experiments were disrupted earlier to spare the animals. Empty circles = females, filled circles = males; the line represents the mean value of both sexes

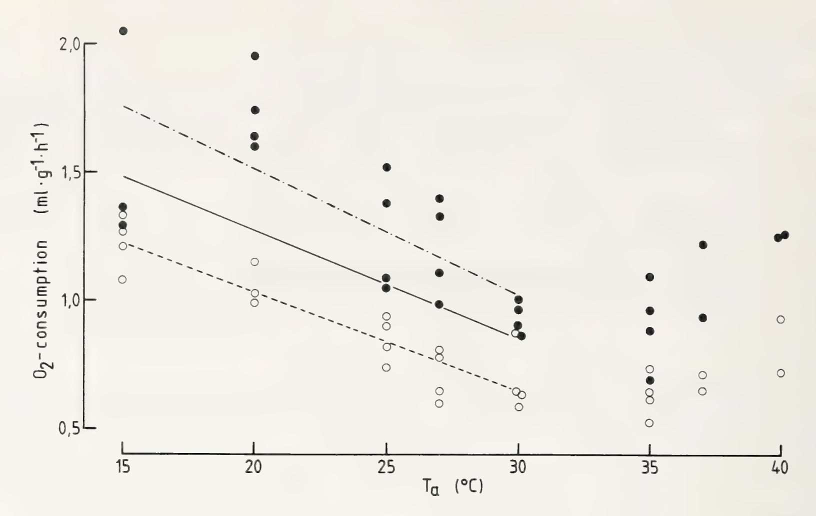


Fig. 3. Oxygen uptake at ambient temperatures from 15–40 °C (calculated mean after an equilibration time of ca. 2 hours; empty circles = females, filled circles = males). Lines represent regression lines for the increase of O_2-consumption at temperatures below the TNZ: ------ = ♀♀: Y (ml O_2/g·h) = 1,795 – 0,038·T_a (°C); r = −0,91; -·-·-· = ♂♂: Y (ml O_2/g·h) = 2,493 – 0,049·T_a (°C); r = −0,73; —— = ♀+♂: Y (ml O_2/g·h) = 2,111 – 0,042·T_a (°C); r = −0,61

T_{re} and T_s at different ambient temperatures under normal caging conditions

In five cuis (3 females, 2 males) we measured T_{re} and T_s at various sites of the body (naked spot above sternal region, inner side of earlaps, hind foot pad, tip of the nose) after exposure to ambient temperatures 15, 22 and 34 °C, respectively (Fig. 4). During these experiments the animals were kept in pairs in their normal cages. After 7.5 h T_{re} and T_s

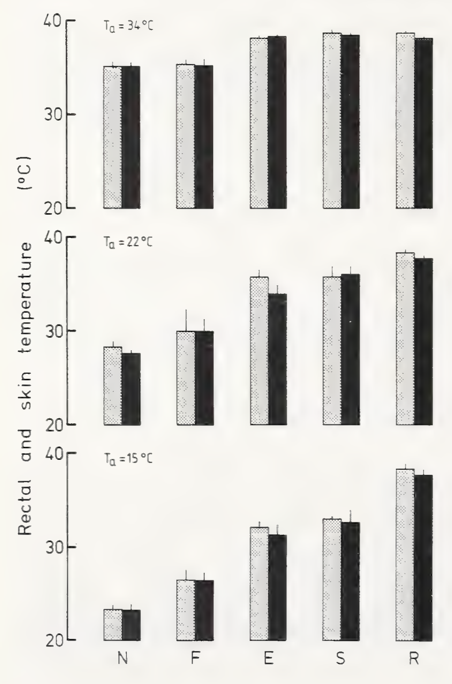


Fig. 4. Skin temperatures at the tip of the nose (N), hind foot pad (F), inner side of earlap (E) and bare patch over sternal region (S) after 3 (left column) and 7 (right column) hours of exposure to ambient temperatures 15, 22 and 34 °C. R = rectal temperature. Height of columns indicates mean value, line indicates S.D. (n = 5; 3 females, 2 males)

were not significantly different from those after 3 hours exposure. At all tested ambient temperatures T_s was lowest at the tip of the nose. The skin temperature of the sternal region and of the earlaps always remained above 30 °C. It fell below this level at the tip of the nose at T_a 22 °C and, additionally, at the hind foot pad at T_a 15 °C suggesting an energy saving reduction of the heatflow to these parts of the body at lower ambient temperatures.

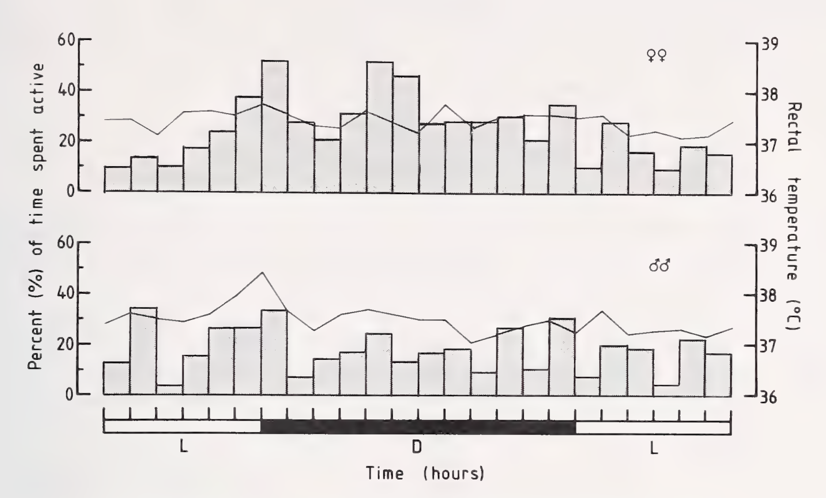


Fig. 5. Nycthemeral variation of time spent active. Mean values calculated for periods of 60 min. The animals were observed with an infrared video device in their normal cages. Each couple was watched twice for a full 24 h period. Lines represent nycthemeral variation of rectal temperature (see Fig. 1)

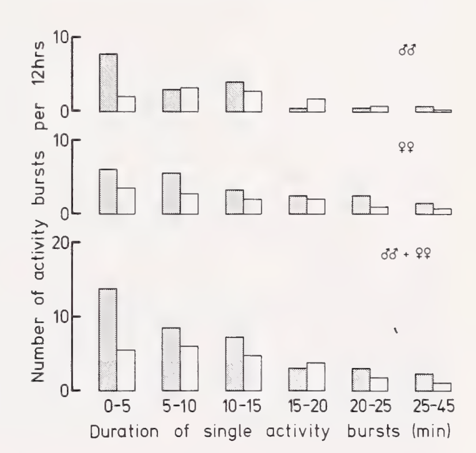


Fig. 6. Relationship between frequency and duration of single activity bursts during D-phase (dotted columns) and L-phase (empty columns)

Activity pattern under normal caging conditions

In the males no obvious nycthemeral variation of the activity pattern could be detected (Fig. 5). Periods of increased activity were rather uniformly distributed over L- and D-phase. If at all, longer lasting periods of increased activity in the male sex occurred before and shortly after switching the lights off and then again during the first half of the D-phase.

The females, on the other hand, showed a different pattern of activity: Two marked peaks occurred at the beginning and at the end of the first half of the D-phase. Whereas the activity level remained fairly high throughout the whole D-phase it was markedly lower

when the lights were on. During the L-phase both sexes spent about the same time active (17.4 % and 17.5 %, respectively). During the D-phase, however, activity increased to 32.9 % of the total time in the females and to only 18.5 % in the males.

Durations of single activity bursts were also somewhat different in both sexes (Fig. 6). Whereas the males preferably were active for periods shorter than 15 min (with a clear maximum of activity bursts ≤ 5 min during the D-phase) the females showed a much stronger tendency for extended periods of activity (duration ≥ 15 min). Visual observation revealed that almost any activity burst was accompanied by the intake of food. Drinking, on the other hand, was almost never seen.

Discussion

The most striking results of our investigations certainly are the marked sexual differences in the level of heat production and in the pattern of daily activity. As yet it is unclear why the basal metabolic rate of female cuis is much lower than that of males (0.69 vs 0.94 ml O_2/g·h at T_a 30 °C). It must be emphasized that this difference in heat production was found at all tested ambient temperatures although rectal temperatures differed only slightly between the sexes.

Sexual differences in heat production have also been reported for a gerbil, *Gerbillus perpallidus* (Müller 1985). However, in this desert species BMR was lower in the male sex which, additionally, had also a lower rectal temperature. Reliable information about different levels of heat production among the sexes of other species is unfortunately missing. One can, therefore, only speculate if the peculiarities in the energetics of gerbils and cuis are related to their different reproductive strategies. The higher levels of heat production and rectal temperature in the females of the altricial gerbils could allow a relatively faster development of the young ones during the prenatal period.

The differences in the energetics of female and male cuis are probably also reflected in their different activity patterns. Our observations revealed that female cuis spend substantially more time active than males, the increased activity almost entirely occurring during the D-phase. It seems possible that the lower basal heat production in the females is an adaptation to keep their daily energy expenditure at a level similar to that of the males in spite of their increased activity. This view is again corroborated by findings in *Gerbillus perpallidus* where preliminary results suggest a lower level of activity in the females which – in this species – show a higher rate of basal heat production than males (Müller 1985 and unpubl. observ.).

Our results indicate a clearly polyphasic activity pattern of cuis in both sexes. Activity bursts occur distributed over the entire 24 hours period. As stated above, however, the females are almost twice as active during the night than during the day. This finding is contradictory to Rood's (1972) and Weir's (1972) observations. These authors classify cuis as being day-active. However, Rood watched his animals only for two hours in the morning and again in the evening. This limited observation time probably does not allow to obtain a detached view of the entire nycthemeral rhythm. Measuring the composition of the urine, on the other hand, Bellamy and Weir (1971) concluded that cuis should be night-active. From the data available at the moment it seems most probably that cuis are polyphasic with a rather uniformly distributed activity in the males (with a small peak around the transition from L-phase to D-phase) and a clear accentuation of activity during the D-phase in the females.

A comparison of our results with those obtained from guinea pigs is rendered difficult because investigations in this species have either only been made with males or the authors do not state the sex of their animals. However, as pointed out above there may exist marked differences between the sexes with regard to activity levels, activity patterns and

heat production. Further studies in guinea pigs and related species dealing with these subjects should carefully watch this fact.

Even a comparison of male cuis with male guinea pigs is difficult because there is considerable discrepancy among authors concerning the nycthemeral rhythm of cavies. From their observations of animals living under natural or near-natural environmental conditions FUCHS (1980), KING (1956), and PEARSON (1951) concluded that guinea pigs are predominantly day-active. Also KAYSER and HILDWEIN (1974) reported a tendency towards day-time activity in caged animals. NICHOLLS (1926) found an almost uniform distribution of the locomotor activity during both D- and L-phase. Her findings were supported by measurements of the sleep-wake states which exhibited a polyphasic pattern throughout the entire 24 h period (PELLET and BÉRAUD 1967). On the other hand, STUPFEL et al. (1981), measuring locomotor activity and CO_2-production, found evidence that guinea pigs are significantly more active during the night-time. BÜTTNER and WOLLNIK (1982) obtained similar results and, additionally, found a well-marked peak of activity around the L:D-transition. In a recent paper JILGE (1985) reported peaks of activity around the L:D- and D:L-transition with a less pronounced peak around the mid of the D-phase. In his experiments activity was generally somewhat higher during the L-phase. It remains unclear if these contradictory findings occur due to a broad genetic variability of rhythmic components in the guinea pig as suggested by BÜTTNER and WOLLNIK (1984) or must be ascribed to different methodological approaches used by the various authors.

In view of this situation it seems that – regarding the males only – our results in the cuis agree most with those of JILGE (1985) in male guinea pigs. It would be very interesting to see if female guinea pigs exhibit the same different activity pattern as has been found in female cuis and if it is also connected with similar peculiarities in their basal energetics. As long as this information is missing it remains difficult to understand the adaptive value of the sexual differences found in cuis.

Acknowledgement

We are indebted to Dr. D. BÜTTNER, Essen, for critically reviewing an earlier draft of the paper.

Zusammenfassung

Aktivitätsmuster und Temperaturregulation beim Wieselmeerschweinchen
(Galea musteloides Meyen, 1833)

Untersucht wurden an sieben Wieselmeerschweinchen *(Galea musteloides)* basale Wärmebildung, temperaturregulatorische Reaktionen und täglicher Aktivitätsverlauf. Bei weiblichen Wieselmeerschweinchen lag die mittlere Rektaltemperatur am Tage und in der Nacht bei 37,3–37,4 °C. Bei den Männchen zeigte sich dagegen ein deutlicher Gipfel zur Zeit des Überganges von der L- zur D-Phase. Im Bereich von T_a 15–35 °C wurde T_{re} zwischen 36,5–38,5 °C reguliert. Aufenthalt bei höheren Temperaturen führte zu einem raschen Anstieg von T_{re}. Der Sauerstoffverbrauch war am niedrigsten zwischen 30–35 °C; der Basalstoffwechsel der Weibchen lag dabei sehr viel niedriger als bei den Männchen (0,69 gegenüber 0,94 ml/g·h). Diese Werte liegen 17 % unter (Weibchen) bzw. 15 % über (Männchen) den gewichtsspezifischen Erwartungswerten. Auch die Zunahme des O_2-Verbrauchs bei Temperaturen unterhalb der TNZ verlief bei den Weibchen deutlich flacher: Die Steigung der Regressionsgeraden war 30 % (Weibchen) bzw. 12 % (Männchen) geringer als der errechnete gewichtsspezifische Wert für die Wärmedurchgangszahl. Messungen der Hauttemperatur an verschiedenen Körperteilen ergaben, daß in kalter Umgebung der Wärmefluß zur Peripherie hauptsächlich im Bereich der Nasenspitze und der Fußsohlen reduziert wird. Unter normalen Haltungsbedingungen unterschieden sich die Aktivitätsmuster der Geschlechter deutlich. Während bei den Männchen die Aktivität ziemlich gleichmäßig über D- und L-Phase verteilt war, zeigten die Weibchen während der Nacht fast eine Verdoppelung der Aktivität. Außerdem war bei ihnen eine stärkere Tendenz zu länger andauernden Aktivitätsschüben zu erkennen.

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Z. Säugetierkunde 53 (1988) 349–357

ISSN 0044-3468

Die Bedeutung des Untergrundes für die Größe von Bauen des Dachses *(Meles meles)* am Beispiel zweier Gebiete Südostbayerns

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Eingang des Ms. 23. 6. 1987

Abstract

The importance of soil composition for the size of badger setts (Meles meles), in two areas in SE Germany

The aim of this study was to analyse the soil composition at the sites where badgers dig their setts and to determine which soil composition they prefer.

148 sets in two areas, the Bavarian Alps and in the alpine foot hills were analysed.

A subjective 4 category scale was used to describe the ease of digging the soil. Setts in the two areas were distributed differently over the categories and in setts in rocks and setts in soil.

Most badger setts were dug in soils containing nearly 10 % clay, 15 % silt and 75 % fine sands. Sandy soils were favoured by badgers ($\chi^2 = 36.86$, $p < 0.001$) and here the most extensive setts were found (H-Test, $p < 0.001$).

Einleitung

Dachse sind nicht gleichmäßig über ihre Habitate verbreitet, dies mag u.a. auch an der Eignung der Böden zum Graben von Bauen liegen. Die Meinungen über die von Dachsen bevorzugten Bodenarten sind nicht einhellig. Viele Autoren gehen auf den ökologisch bedeutsamen Faktor Boden nicht oder nur am Rande ein. Die Verwendung von regional eng begrenzt vorkommenden Bodenbezeichnungen erschwert darüber hinaus eine Vergleichbarkeit in größerem Rahmen. Nach Stubbe (1982) bevorzugen Dachse tiefgründige, schwere Böden. Neal (1977) nennt vor allem sandige Böden als bevorzugtes Substrat für die Bauanlage, weil dieses gut dräniert und leicht zu graben ist. Zu ähnlichen Aussagen kommen auch Dunwell und Killingley (1969) sowie Likhachev (1956), der zeigte, daß die Kessel, wenn möglich, in sandigem Substrat angelegt werden. Neal (1977) berichtet ferner, Baue in Sandböden wären vorhersagbar viel größer als Baue in anderen Böden. Ein objektives Kriterium, nach welchem die Baugrößen festgestellt wurden, teilt er indes nicht mit.

In der vorliegenden Studie wird versucht zu belegen, daß die voneinander abweichenden Baugrößen zweier getrennter Untersuchungsgebiete auf die unterschiedliche Eignung der Böden zur Bauanlage zurückzuführen sind.

Untersuchungsgebiete

Die in Südostbayern gelegenen Untersuchungsgebiete sind das Salzachhügelland – ein Teil des Alpenvorlandes – und der Raum des Berchtesgadener/Ramsauer-Beckens, zu den nördlichen Kalkalpen gehörend. Die südlichen und östlichen Teile des Berchtesgadener/Ramsauer-Beckens liegen z.T. im Nationalpark Berchtesgaden, dessen Nordrand einen Schwerpunkt des Untersuchungsgebietes darstellte.

Würmeiszeitliches Moränenmaterial, von Grobschottern bis zu Feinsanden mit unterschiedlichen Beimengungen von Ton und Schluffen, bildet die vorherrschenden Böden des Alpenvorlandes. Die Wälder sind auf die für eine landwirtschaftliche Nutzung wenig günstigen Moränenhügel, die

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Flußauen oder vermoorte Niederungen reduziert. Grünlandwirtschaft und Ackerbau sind die vorherrschenden landwirtschaftlichen Nutzungsformen.

Das Berchtesgadener/Ramsauer-Becken ist durch relativ weite und reich strukturierte Talzonen charakterisiert. Flachgründige, wenig fruchtbare Böden sind vorherrschend, sie erlauben nur eine Mäh- und Weidenutzung. Der Waldanteil ist mit ca. 50–60 % ziemlich hoch.

Material und Methode

Es wurden 148 Dachsbaue (Haupt- und Nebenbaue, davon 73 Erdbaue, 61 Felsbaue und 14 Baue unter Hütten, Ablaufröhren etc.) untersucht und ihre Größe ermittelt. Als sehr brauchbar erwies sich dabei das Bestimmen ihres Rauminhaltes unter Zuhilfenahme der davor liegenden Erdauswurfhaufen und einer hierauf aufbauenden Einteilung in Größenklassen, die auch eine Einteilung in Haupt- und Nebenbaue erlaubt (vgl. Bock 1986). Nur die Naturbaue (= Erd- und Felsbaue) werden im weiteren behandelt, da Baue in anthropogenen Strukturen für die angewendeten Beurteilungskriterien keine brauchbaren Daten liefern.

Mit einer Grabgabel wurden die Erdauswurfhaufen zum Sammeln von Knochen durchwühlt und die Böden dabei auf ihre Grabbarkeit hin beurteilt. Diese rein subjektiv bewertenden Befunde wurden in vier Grabbarkeitsklassen eingeteilt: Klasse 1 = schlecht bzw. nicht grabbar, 2 = mäßig, 3 = gut und 4 = sehr gut. In diese Grabbarkeitsbewertung sind auch die Felsbaue einbezogen.

Von 30 repräsentativen Bauen (8 im Gebirge, 22 im Alpenvorland) wurden Bodenproben aus den Erdauswurfhaufen entnommen und auf Bodenart, Körnung und ihre Eigenschaften (= Bonitierung) und ihre Grabbarkeit hin untersucht. Diese Proben erlaubten durch Vergleich die Zuordnung der restlichen Bodenproben. Im Hinblick auf ihre Grabbarkeit wurden die Werte der Bodenanalyse nur zum Teil berücksichtigt, da z.B. grobe Gesteinsbrocken, die einem Dachs das Graben schwer machen, in den Analysewerten nicht zum Ausdruck kommen.

Tabelle 1. **Grabbarkeit des Untergrundes in beiden Untersuchungsgebieten sowie getrennt nach Fels- und Erdbauen**

Grabbarkeitsklasse	4 (sehr gut)	3 (gut)	2 (mäßig)	1 (schlecht)
Gesamt n	38	24	46	26
Gebirge				
Felsbau %	0	6	44	50
Erdbau %	0	47.4	47.4	5.3
Alpenvorland				
Felsbau %	0	0	100	0
Erdbau %	69.1	21.8	9.1	0

Ergebnisse

Die Baugrößen

Die Baugrößenunterschiede der beiden Untersuchungsgebiete sind drastisch. Die durchschnittliche Größe der Alpenvorlandbaue (n = 65) liegt bei 12 m^3 Rauminhalt, die der Gebirgsbaue (n = 69) bei 0,5 m^3 (Mann-Whitney U Test, $p < 0{,}001$).

Die Grabbarkeit der Böden

Nur selten war es möglich, die Grabbarkeit des Bodens am gewachsenen Untergrund zu bestimmen. Deshalb wurde das aus dem Bau gescharrte Bodenmaterial der Naturbaue getrennt nach den beiden Untersuchungsgebieten, in vier Grabbarkeitsklassen eingeteilt, sowie nach Fels- und Erdbauen getrennt (vgl. Tab. 1). In ihrer Grabbarkeit unterscheiden sich die Baue beider Gebiete deutlich ($\chi^2 = 69{,}507$, $p < 0{,}001$).

Diese Grabbarkeitsbestimmung der Böden vor Ort wurde durch die späteren Bodenanalysen ergänzt.

Die Bodenanalysen des Erdauswurfmaterials

Im Gebirge waren Bodenanalysen nur bei einigen Erdbauen (n = 8) sinnvoll, da bei der großen Zahl von Felsbauen nur das Material der Spaltenfüllungen zu bestimmen ist, welches aber nicht mit dem tatsächlichen Material der Baue identisch ist. Mitunter kann es auch bei Erdbauen vorkommen, daß das von den Dachsen herausgegrabene Material dem Beobachter nur in Form dieser Erdauswurfhaufen und nicht als anstehendes Material

Tabelle 2. **Analyse von 30 Bodenproben aus Dachsbauen**
A = Alpenvorland, B = Gebirge

Nr.		Körnung (%)			BA§	Bonitierung[1]					
		#T	U	S		a	b	c	d	e	f
A											
1	(1)	15	15	70	l̄S	5	3	1	3	5	3
2	(1)	10	45	45	ulS	5	2	2	5	5	4
3	(1)	10	15	75	lS	5	3	4	5	4	3
4	(1)	5	10	85	u'S	5	2	1	5	5	2
5	(1)	8	12	80	l'S	5	2	3	3	5	3
6	(1)	5	10	85	l'S	5	2	4	5	3	2
7	(1)	8	15	77	l'S	0	3	5	5	1	3
8	(2)	0	10	90	S	5	1	0	5	5	1
							0*				
9	(2)	5	5	90	S	5	4	4	2	0	1
10	(2)	20	75	5	l̄U	5	4	4	4	3	4
11	(2)	25	70	5	l̄U	0	4	5	4	1	4
12	(2)	15	70	15	lU	5	3	1	5	5	4
13	(3)	40	58	2	utL	3	4	5	4	0	4
14	(3)	25	65	10	t̄L	5	4	4	4	3	4
								5		0&	
15	(3)	35	50	15	ūT	4	4	5	4	0	4
16	(3)	30	60	10	uL	0	4	5	5	1	4
17	(3)	20	75	5	l̄U	1	3	5	4	0	4
18	(3)	15	80	5	lU	0	4	5	5	0	5
19	(3)	15	55	30	slU	4	3	5	4	1	3
20	(3)	35	55	10	utL	3	4	5	4	1	4
21	(4)	0	0	0	H	0	3	4	5	5	5
22	(4)	0	0	0	H	0	5	5	5	2	5
B											
23	(2)	25	70	5	l̄U	0	3	4	4	3	4
24	(2)	10	10	80	lS	5	2	4	3	2	2
25	(2)	25	70	5	t̄U	3	4	5	4	4	4
26	(2)	15	75	10	lU	1	3	5	5	3	4
27	(2)	15	80	5	lU	1	4	4	5	3	4
28	(2)	25	70	5	l̄U	0	4	5	4	2	4
29	(3)	35	60	5	utL	0	4	5	4	1	4
30	(3)	45	55	0	utL	4	4	4	3	2	3

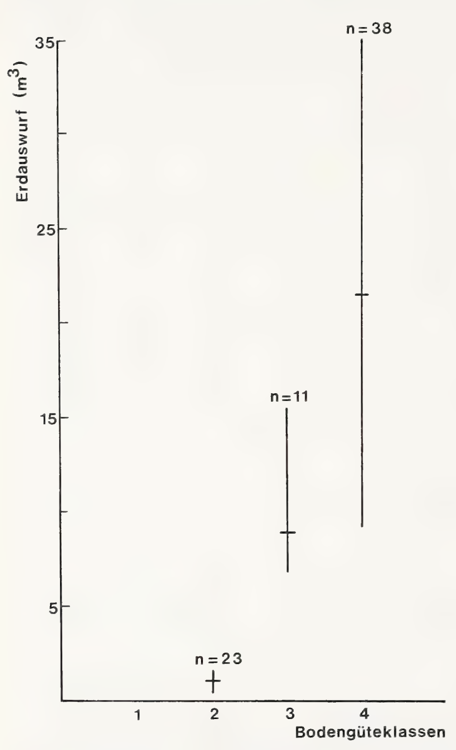
Die Zahlen in den Klammern geben die Bodengüteklassen wieder, hierbei wurde auch größeres Gesteinsmaterial berücksichtigt, das in der Bodenanalyse nicht aufscheint. Körnung = % Anteile der verschiedenen Bodenarten in einem Bodengemisch; T = Ton, U = Schluff, S = Sand, L = Lehm, H = Humus, # TUS = Ton-, Schluff- und Sandgehalt; BA§ = Bodenart nach Bodenkundlicher Kartieranleitung, 3. Aufl. (1983); l' = schwach lehmig, l̄ = stark lehmig, t' = schwach tonig, t̄ = stark tonig; u' = schwach schluffig, ū = stark schluffig; [1]a = Carbonatgehalt, b und c = Standfestigkeit des Bodens in feuchtem bzw. trockenem Zustand, d und e = Grabbarkeit des Bodens in feuchtem bzw. trockenem Zustand, f = Wasserhaltefähigkeit des Bodens; 0 = nicht, 1 = sehr gering/schlecht, 2 = gering/schlecht, 3 = mäßig, 4 = gut/hoch, 5 = sehr gut/hoch; & = die in 2. Zeile stehenden Werte gelten für toniges Material; * = in fast wassergesättigtem Zustand zerfließend.

zugänglich ist. In jedem Falle ist daher bei diesem Bautyp die Bestimmung der Böden durch Analyse der Erdauswurfhaufen aussagekräftig.

Im Alpenvorland wurde der Erdauswurf von 22 Dachsbauen analysiert. Die Ergebnisse der Bodenanalyse aus beiden Untersuchungsgebieten sind in Tab. 2 aufgeführt.

Die größten Bauanlagen des Alpenvorlandes liegen alle in lehmigem Sand. Bei solcher Bodenzusammensetzung sticht für gewöhnlich auch die Größe der Auswurfhaufen ins Auge. Die Grabbarkeit dieser Böden ist sehr gut, wenn sie nicht zu skelettreich sind (als skelettreich werden Böden bezeichnet, die viele anorganische Teilchen >2 mm enthalten). Sie trocknen rasch ab, erwärmen sich schnell und gewährleisten eine geringe Restfeuchte im Innern der Baue. Eindringendes Wasser versickert im allgemeinen schnell. Ist der Tonanteil dieser Sandböden sehr gering, dann hat dies auch nachteilige Folgen. Die geringe Wasserhaltefähigkeit dieser Böden (s. z.B. Tab. 2 Nr. 9) bedingt ein sehr schnelles Durchtropfen des Niederschlagswassers. Die Standfestigkeit dieser Böden läßt rasch nach und ihre Fließgrenze wird alsbald erreicht. Zu großes Austrocknen kann andererseits zum Zerrieseln solcher Böden führen.

Böden mit einem geringen Sandgehalt, hohen Ton- und Schluffanteilen werden ebenfalls von den Dachsen bewohnt. Die hohe Wasserhaltefähigkeit dieser Böden hat zur Folge, daß sie viel Niederschlagswasser aufnehmen können, bevor Wasser durchtropft oder ihre Standfestigkeit merklich nachläßt. Auch bleibt, je nach Skelettanteil des Bodens, eine gute Grabbarkeit über einen langen Zeitraum erhalten. Austrocknung kann bei bindigen Böden das Graben in den äußeren Bodenschichten sehr erschweren bzw. sogar ganz verhindern. Gleichzeitig sind diese Böden relativ kalt, und sie erwärmen sich nur langsam. Da eingedrungenes Wasser nur langsam versickert, bewirkt dies über einen langen Zeitraum eine hohe Restfeuchte in den Bauen.



Die Baugrößen in Abhängigkeit von der Bodengüte. (Bodengüteklasse 1 s. Text)

Die Beziehung zwischen Bodenmaterial und Baugröße bei Erdbauen

Die Böden beider Untersuchungsgebiete wurden in vier Qualitätsstufen eingeteilt (Felsbaue werden gesondert behandelt).

Als „schlecht" (= 1, die niedrigste Bewertungsstufe) werden Torfböden und grobe Moränenschotter bezeichnet. „Mäßig" (= 2) sind Tone und Schluffe mit zum Teil schieferigen Gesteinsbrocken. „Gute" Böden (= 3) sind skelettreiche Sande aller Art und „sehr gute" Böden (= 4) sind Feinsande mit geringen Ton- und Schluffanteilen. Wie bei allen künstlichen Einteilungen, so gibt es auch hier zwischen den einzelnen Gruppen Übergänge.

In der Abbildung sind die Baugrößen zu den vier Bodengüteklassen in Beziehung gesetzt. Daraus ergibt sich klar, daß Dachse lieber in Sandböden als in anderen Böden graben ($\chi^2 = 36{,}86$, $p < 0{,}001$) und in diesen Böden die größten Baue anlegen (H-Test, $p < 0{,}001$). (Da die Bodengüteklasse 1 nur zwei Werte enthält, war es nicht möglich, sie in der Abbildung darzustellen.)

In der stark verinselten Landschaft des Alpenvorlandes fällt die beschränkte Siedlungsmöglichkeit für Dachse auf. Selbst in Wäldern sind Dachsbaue oftmals mangels geeigneter Böden nur an ganz bestimmten Stellen zu finden, meist handelt es sich hierbei um Sandböden würmeiszeitlicher Jungmoränen. Es gibt Gebiete, in welchen sich ein großer ganzjährig bewohnter Hauptbau befindet, beständige Nebenbaue sind aber nirgends im Streifgebiet dieser Dachse zu finden. In trockenen Zeiten werden dann Ablaufrohre bezogen und wenn der Mais oder das Getreide eine bestimmte Höhe erreicht haben, legen die Dachse alljährlich an den selben Stellen im Feld Baue an, die genau so regelmäßig von den Bauern wieder zerstört werden. Im Untersuchungsgebiet sind bisher drei solcher Stellen im Feld bekannt.

Zwei Baue wurden in Moorgebieten untersucht. In beiden Fällen steht der Grundwasserspiegel sehr hoch, so daß zwischen Erdoberfläche und Grundwasserspiegel für die Bauanlage höchstens eine 90 cm tiefe Bodenschicht bleibt. Beide müssen wegen der unzureichenden Boden- und Standortverhätlnisse, der hohen Wasserhaltefähigkeit des Bodens und auch von ihrem Raumangebot her zu den schlechten Bauen gerechnet werden.

Die spezielle Situation der Felsbaue

Viele Felsbaue verfügen nur über ein begrenztes Hohlraumangebot, weshalb in diesen eine multifunktionale Nutzung (Überwinterung, Jungenaufzucht, Bewohnen verschiedener Bauteile je nach Bedarf), wie in „guten" Erdbauen nicht möglich ist (vgl. Bock 1986). Die Felsbaue sind in drei Typen einzuordnen: Felsblöcke, Kalksteinfelswände und Konglomeratfelswände bzw. -blöcke. Als Felsblöcke werden freistehende bzw. -liegende Felsen bezeichnet, deren Begrenzungen gut erkennbar sind. Ist die Längen- oder Breitenausdehnung eines größeren Blockes nicht erkennbar, weil sich ein Teil davon in den Hang fortsetzt, so wird er als Felswand eingestuft. Im Alpenvorland sind Konglomeratfelswände die alleinig vorkommenden Felsbautypen (n = 10), sie nehmen nur 15,4 % der hier gefundenen Naturbaue ein.

Felsblockbaue sind im Gebirge eine häufige Bauvariante (n = 30). Nur unter zweien wurden im Beobachtungszeitraum Junge nachgewiesen. Beide Felsbaue heben sich mit drei weiteren in ihren Ausmaßen deutlich von der Anzahl der übrigen Baue ab (Seitenlänge 10 bis 15 m). Ein Überwintern mit Jungenaufzucht dürfte nur unter diesen großen Felsblökken möglich sein.

Kleine Blöcke (n = 25) haben im Durchschnitt folgende Ausmaße: L = 5 m, B = 3,4 m, H = 3 m. Der Hohlraum, welchen sich die Dachse im günstigsten Falle darunter anlegen können, ist in allen Fällen nur zum Übertagen im Sommerhalbjahr geeignet. Nur dreimal waren im Winter unter derartigen Blöcken Tiere für höchstens einen Tag festzustellen.

Bei einer Anzahl kleiner Blöcke, unter denen telemetrierte Dachse im Sommerhalbjahr übertagten, war deren Reaktion auf den sich annähernden Untersucher gut zu vernehmen. In einem Fall war sogar der abwartende Dachs, der aus dem Lager an den entferntesten Punkt seiner Behausung geflüchtet war, durch das Eingangsloch zu beobachten.

Felswandbaue (n = 29), deren größtmögliche Hohlraumdimensionen sich der Beurteilung eines Untersuchers völlig entziehen, können in ihren Baumaßen ausschließlich näherungsweise über die Erdauswurfhaufengrößen beurteilt werden ($\tilde{x}$ = 3,5 m^3). Vergleicht man die Größen von Felswand-Hauptbauen (n = 18) und Erd-Hauptbauen (n = 40) nach ihren Erdauswurfhaufen, so liegen die Felswand-Hauptbaue im Mittel ($\tilde{x}$) bei 6,2 m^3, und sind somit deutlich kleiner als die Erd-Hauptbaue mit 21,4 m^3 (Mann-Whitney U Test, $p < 0{,}001$).

Von den sieben Konglomeratfelswänden im Gebirge sind sechs Hauptbaue, die von ihren Hohlraummaßen her mit zu den besten Bauen gehören. Doch sind hierunter auch drei sehr feuchte Baue, von denen zumindest einer zur kalten Jahreszeit in Teilen

unbewohnbar ist. Das durch die Decken tropfende Wasser gefriert in den Eingängen zu Eissäulen, wodurch diese für lange Zeit unpassierbar sind.

Die ursprünglichen Bodenmaterialien, die aus diesen Bauen gescharrt wurden, sind häufig infolge des darin enthaltenen Humusanteils, der vom Nestmaterial herrührt, nicht mehr mit Bestimmtheit zu ermitteln. Außerdem gilt es hier in erster Linie den Fels zu beurteilen, da es sich bei dem Bodenmaterial in vielen Fällen um Spaltenfüllungsmaterial handelt. Bei vielen Felsbauen – insbesondere bei Konglomeratfelsen – bestehen die zeitlich jüngeren Grabmaterialien, neben dem verrotteten Nestmaterial, fast nur aus grobem Geröll, welches bis zu kindskopfgroße Gesteinsbrocken enthält.

Bei den Konglomeratfelsbauen des Alpenvorlandes besteht das Erdauswurfmaterial zum überwiegenden Teil aus schluffig-tonigem Lehm sowie dem humosen Material der zersetzten Nestlaubstreu. Diese Böden sind wegen der in ihnen enthaltenen Dauerfeuchtigkeit nur bewohnbar, weil sie durch die Felsplatte abgedeckt sind. Dennoch ist die Mehrzahl dieser Baue während des Sommerhalbjahres kaum bewohnt.

Einen Übergang vom Erd- zum Felsbau stellen solche Baue dar, deren Hohlräume blockgestützt sind. Größere sich ineinander verkeilende Blöcke, wie sie z.B. als Folge von Bergstürzen entstehen, bilden Hohlräume in einem sonst völlig unbewohnbaren Bodenmaterial.

Diskussion

In beiden Untersuchungsgebieten sind – von Felsdecken einmal abgesehen – stabile, wasserundurchlässige Deckschichten bei Dachsbauen selten. Unter einer humosen Bodenschicht von wenigen Zentimetern im Gebirge, bis zu 30 cm im Alpenvorland findet sich im allgemeinen jene Bodenschicht, in welcher auch der Bau angelegt wird. Da die Mehrzahl der Baue am Hang liegt, besteht auch bei Sandböden mit geringen Ton- und Schluffgehalten kaum Einsturzgefahr. Ein Großteil des Regenwassers läuft infolge des Gefälles bereits oberirdisch und in der Mutterbodenschicht ab. Weiteres Wasser rinnt entlang den Decken der Kessel und Eingangsröhren ab. Das restliche Wasser, das durch den Kessel tropft, kann das Nest bzw. darinliegende Dachse benetzen. Da aber in allen Bauen die hohe Luftfeuchtigkeit eine Verdunstung erschwert, muß eindringendes Wasser möglichst schnell wieder aus dem Kessel abgeleitet werden. Diese Möglichkeit ist bei sandigen Dachsbauen mit und ohne wasserundurchlässiger Deckschicht gegeben. Bei feuchtigkeitsgesättigter Luft ist es in allen Bautypen gleichermaßen schwierig für die Dachse, ein nasses Fell zu trocknen. Die einzige Möglichkeit – abgesehen von Zugluft, die die meisten Tiere meiden – ist das Trocknen von Fell und Nest durch die Körperwärme.

In ebenem Gelände, wo schwerere Böden vorherrschen, können die Dachse, abgesehen von einer Eignung des Bodens, meist deshalb nicht siedeln, weil diese Gebiete ausschließlich einer landwirtschaftlichen Nutzung vorbehalten sind und die Landschaft hier in aller Regel einförmig flach ist. Hier wurden durch die Flurbereinigung die Verteilungsmuster der Dachsbaue und daraus resultierend die der Dachse so entscheidend verändert, daß eine rein anthropogen bedingte Verteilung vorliegt. Dachse sind keine primären Waldbewohner, sie besiedeln auch Halbwüsten und Steppen (vgl. Heptner und Naumov 1974). Mehrere Baue im Gebirge liegen an waldlosen Abhängen, doch auch um diese stellt sich bald eine nitrophile Pioniervegetation mit Holunder *(Sambucus nigra)* und Brennessel *(Urtica dioica)* ein, die durch die Ausscheidungen der Dachse und deren Erdbewegungen gefördert wird.

Lugert (1985) führt die auf den Wald beschränkte Verteilung der Dachsbaue in Schleswig-Holstein auf Störung und Verfolgung zurück. Kruuk (1978) zeigt für die Wytham Woods bei Oxford, daß die dortigen Dachse ihre Hauptbaue zwar alle in sandigen Böden anlegen, diese aber zugleich im Wald liegen.

Nicht so sehr direkte Verfolgung, als vielmehr die Zerstörung eines Teils seiner Lebensräume ist für das Siedeln des Dachses im Wald verantwortlich zu machen.

Interessant sind die detaillierten Angaben LIKHACHEV's (1956) über die verschiedenen Bodenprofile bei den von ihm ausgegrabenen Dachsbauen südlich von Moskau. Lehme sind bis in ca. 130 cm Tiefe die hier vorherrschenden Böden. Sie machen für die Dachse ein Vordringen in die tieferen Bodenschichten recht schwierig. An Abhängen, wo die Bodenschichten durch Gewässerläufe angeschnitten sind, können die Dachse genau jene tieferliegenden sandigen Bodenschichten angraben, die zur Bauanlage am geeignetsten sind. LIKHACHEV's Schlußfolgerungen, die Baue würden unter dem Grundwasserniveau liegen, dürften nur bei Schichtböden mit verschiedenen Grundwasserniveaus zutreffen. Früher oder später würden derartige Bauanlagen bei wechselnden Grundwasserständen überflutet werden, wenn die Dachse versuchen, die darüberliegenden Decken zu durchstoßen. Periodisch wiederkehrende Staunässe wäre hier eher vorstellbar. In einer Reihe von Dachsarbeiten aus England werden Angaben zu den Böden gemacht, in welchen die Baue gegraben wurden. DUNWELL und KILLINGLEY (1969) sowie NEAL (1972) halten eine wasserundurchlässige Deckschicht und eine darunterliegende Sandlage am besten zum Anlegen von Bauen geeignet. Von der großen Anzahl an Dachsbauen, die HARRIS (1984) im Bereich der Stadt Bristol bearbeitete, lag der überwiegende Anteil ebenfalls in Sandstein bzw. sandigem Boden. CLEMENTS (1974) zeigt, daß die Dachse, wenn sie die Wahl haben, immer Sandböden bevorzugen. Aus den von GOETHE (1955) vorgestellten Untersuchungen ist klar zu erkennen, daß es sich in seinen Untersuchungsgebieten Teutoburger Wald und Lipperland um suboptimale Böden im obigen Sinne handelt. Die meisten der von ihm registrierten Baue befanden sich in Lehm und Keupermergelböden. Die Annahme, daß die Mehrzahl der dort gefundenen Baue suboptimal ist, wird durch die für diese Gebiete genannten Nebenbaue in Feldern – hier „Feldnotbaue" genannt – erhärtet.

Bei Felsbauen ist das ausgegrabene Bodenmaterial für eine Baubeurteilung in anderer Hinsicht interessant. Analysiert man hier die Auswurfhaufen, so findet sich in der unteren Schicht jenes Material, aus welchem die ursprüngliche Spaltenfüllung des Felsgesteins bestand. Darüber liegen humose Erdschichten, die in ihren obersten Lagen zum Teil aus nicht verrottetem Pflanzenmaterial bestehen. Dies ist insbesondere dann der Fall, wenn die Nesteinstreu vorwiegend aus Buchenlaub zusammengetragen wurde.

Auf ein in vielen Fällen sehr begrenztes Hohlraumangebot der Felsbaue kann aus zwei Gründen geschlossen werden: Erstens sind hier über die Jahre keine oder nur sehr geringe Grabaktivitäten zu bemerken und zweitens sind vor diesen Bauen häufiger Skelettreste von verendeten Dachsen zu finden. Die Gesteinsbrocken, die im Gebirge vor allem im Auswurfmaterial vor Konglomeratfelsbauen zu finden sind, zeigen, daß hier das Raumangebot voll ausgeschöpft wird. Wohnungsnot bei Dachsen kommt aber auch in anderen Untersuchungen zum Ausdruck. WIJNGAARDEN und VAN DE PEPPEL (1964) berichten von bis zu 20 cm großen Gesteinsbrocken, die im Auswurfmaterial der Dachsbaue zu finden sind. Ebenso belegen die bei NEAL (1977) abgebildeten Kalksteinbrocken, auf welchen tiefe, von Dachskrallen herrührende Rillen zu sehen sind, die auch andernorts vorhandene Wohnraumnot der Dachse in felsigem Gelände.

Dort wo Baue kaum anzulegen sind, findet man Dachse auch unter Hütten und in nicht wasserführenden Ablaufröhren. Dies ist besonders häufig im Gebirge der Fall, tritt aber auch im Alpenvorland auf, wo die Habitate der Dachse durch strukturarme Agrarlandschaften eingeengt worden sind.

Vor Erdbauen in „guten Böden" findet man relativ selten die bereits oben erwähnten Überreste verstorbener Dachse. Diese Baue gestatten es den Dachsen, bestimmte Bauteile für einen längeren Zeitraum nicht zu bewohnen, in andere Bauteile auszuweichen oder neue zu graben. Im Gebirge oder in anderen Landschaften, die den Dachsen nur wenig Ausweichmöglichkeiten bieten, ist die Verfügbarkeit genügend guter Baue ein populationsbegrenzender Faktor („gute Baue" sind Baue mit großen inneren Dimensionen und

einer günstigen Bodenzusammensetzung). Die Baue bleiben kaum länger als ein halbes Jahr unbewohnt und Tierleichen müssen wegen Raumnot – meist bald nach der Zersetzung – entfernt werden.

Die Feststellung, die hohe Mortalität der Jungdachse in den ersten Lebenswochen (bis 25 %) sei durch das stickige Bauklima verursacht (Neal und Harrison 1958; Stubbe 1965), kann nur für solche Baue zutreffen, deren über die Maßen feuchtes Baumilieu durch eine hohe Wasserhaltefähigkeit und mangelhafte Drainage des Bodens bei schlechter Belüftung verursacht wird. In erster Linie sind dies Böden mit einem geringen Sandanteil. Baue mit diesen Eigenschaften sind als suboptimal zu werten. Auch wenn einige davon im Laufe der Jahre Ausmaße erreichen, die an die Größe von optimalen Sandbauen heranreichen, so sind hier große Baue im Vergleich zur Häufigkeit großer Baue in Sandböden selten.

Danksagung

Diese Untersuchung wurde z.T. durch Mittel des Bayerischen Staatsministeriums für Landesentwicklung und Umweltfragen finanziert. Herrn Dr. H. H. Becher vom Lehrstuhl für Bodenkunde der TU München danke ich für die Analyse der Bodenproben und Herrn E. Langenscheidt von der Nationalparkverwaltung Berchtesgaden für geologische Auskünfte im Gelände. Den Herren Dr. W. Arnold und Dr. F. Trillmich vom Max-Planck-Institut für Verhaltensphysiologie Seewiesen bin ich für kritische Durchsicht des Manuskripts dankbar.

Zusammenfassung

In zwei Untersuchungsgebieten Südostbayerns wurden 148 Dachsbaue hinsichtlich ihrer Eignung zur Bauanlage untersucht.

Die Baugröße wurde getrennt nach Erd- und Felsbauen ermittelt. Anhand des vor den Bauen liegenden Erdauswurfmaterials wurde die Grabbarkeit des Bodens in vier Grabbarkeitsklassen eingeteilt, worin sich die beiden Untersuchungsgebiete signifikant unterscheiden ($\chi^2 = 69{,}507$, $p < 0{,}001$).

Von 30 Erdbauen wurden Bodenanalysen durchgeführt, wobei u.a. die Körnung, die Bodenart und die Bonitierung des Bodens analysiert wurden. Nach dieser Bodenanalyse, mit deren Hilfe auch die anderen restlichen Böden zugeordnet werden konnten, wurden diese Böden in vier „Qualitätsstufen" eingeteilt und diese mit der Baugröße in Beziehung gebracht. Daraus ergibt sich klar, daß die Dachse Sandböden vor allen anderen Böden bevorzugen ($\chi^2 = 36{,}86$, $p < 0{,}001$) und hier auch die größten Baue anlegen (H-Test, $p < 0{,}001$). Zum Graben eines Dachsbaues eignet sich ein Boden von ungefähr der folgenden Körnung am besten: bis 10 % Tonanteile, 15 % Schluff und ca. 75 % Sand.

Die Typen der Felsbaue und ihre Funktion werden bewertet und die ermittelten Befunde diskutiert. Die Daten sind mit der eingangs aufgestellten Hypothese, daß die unterschiedlichen Baugrößen beider Untersuchungsgebiete auf „Qualitätsunterschiede" der Böden zurückzuführen sind, verträglich.

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Z. Säugetierkunde 53 (1988) 358–364
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ISSN 0044-3468

Scent marking behaviour in captive Water mongooses *(Atilax paludinosus)*

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Receipt of Ms. 1. 7. 1987

Abstract

Scent marking in captive *Atilax paludinosus* is described. The four methods recorded include defaecation, urination, anal marking and cheek rubbing. Anal marking was most frequently used and in females the frequency was significantly higher during the non-breeding season. Sexual dimorphism with respect to anal marking was exhibited, females marking more frequently than males. Cheek rubbing frequency was higher in the presence of conspecifics and females showed a significant increase in cheek marking during the breeding season. Defaecation rates varied with food intake, while urination frequencies were significantly higher when mongooses shared an enclosure with a conspecific. The relevance of the different rates and patterns of marking are discussed in relation to the ecology of solitary *Atilax*, and comparisons with sociable *Helogale* are made.

Introduction

Pocock (1916) was the first to describe the external structure of the anal sac in *Atilax*. More recently interest in mongoose scent glands and their secretions has increased. Gorman (1976, 1980) and Gorman et al. (1974) have analysed the anal secretions of *Herpestes auropunctatus*, and Hefetz et al. (1984) have shown that *Herpestes ichneumon* exhibits sex specificity with regard to its anal gland secretions. In addition marking behaviour has been studied in *Helogale undulata rufula* (Rasa 1973) and *Suricata suricatta* (Moran and Sorensen 1980). Hediger (1949), Fiedler (1957), Michaelis (1972) and Ewer (1973) have described some of the marking behaviour in a variety of herpestines, including *Atilax*.

The current study describes in detail marking behaviour in captive water mongooses. An attempt is made to interpret the meaning of the various marking behaviour patterns and to compare these with patterns in other herpestines.

Material and methods

Eight mongooses (three males and five females) were held captive in outdoor enclosures. Details regarding their housing are presented in Baker and Meester (1986). Observations were made from an observation hide one metre distant from the cages. Marking sequences were either recorded on detailed checksheets or filmed using a National VHS portable video system. Frequency of marking events was analysed for each hour of observation. Sequence analysis was carried out with the aid of transition matrices and flow diagrams were constructed (Chatfield and Lemon 1970; Lehner 1979). A behaviour sequence was delimited by the initial approach to and withdrawal from the object to be marked.

Results

Four methods of depositing scent products were recorded, including defaecation, urination, anal dragging and cheek rubbing. Figure 1 shows the frequency of the different marking patterns. Allomarking was not observed and all marks were deposited on inanimate objects. However, hand-raised mongooses did mark their 'human parent'.

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Defaecation

In 15 different 24-hour periods defaecation occurred twice per individual animal. Mongooses tended to defaecate soon after becoming active in the early evening (between 17h30 and 19h30) and then again in the early hours of the morning (between 05h00 and 06h30) before retiring for the day. Scats were always deposited on specific scat sites or middens. In six out of the eight mongoose enclosures the middens were located at the furthest point from the nestbox, while in the remaining two enclosures the middens were positioned close to the nest site. All defaecation sites were located at ground level and scats were never deposited over tree trunks or on rocks. When two or more animals were housed together, a common midden was used. Once the particular site for defaecation was chosen there was never any change in its location.

Defaecation postures usually involved a simple squat. The tail position was characteristic, extending straight backwards with a slight upward curve along its length. Mongooses often circled a few times before settling to defaecate.

Urination

Urination frequencies varied from zero to 5 times per hour ($\bar{x} = 0.55$, $n = 158$). Urination frequencies were significantly higher when mongooses were housed alone than when they shared an enclosure with a conspecific ($d = 2.47$, $0.02 > p > 0.01$). Urination sites varied and, unlike scat sites, different parts of the enclosures were used, although some sites were preferentially marked such as small rocks, the midden and logs.

Urination was usually performed in a squatting position with the base of the tail positioned slightly higher than during defaecation. Male mongooses regularly lifted a hind leg when urinating, and on occasion females were also noted to use the leg lift. When using the leg lift position the mongooses were apparently not aiming to increase the height of the urine mark, as they did not always lift their legs next to a vertical object.

Anal dragging

Frequency of anal marking varied from zero through 21 times per hour ($\bar{x} = 1.96$, $n = 143$). The presence of known conspecifics had no significant effect on the rate of anal dragging ($d = 0.09$, $p > 0.1$). During the breeding season it was found that while there was no significant difference in anal marking frequency in males ($d = 1.32$, $p > 0.1$) there was a significant difference in females ($d = 4.02$, $0.0001 > p > 0.00001$) with more marking exhibited during non-breeding. Anal scent was deposited on small rocks, nest boxes, tree stumps and tunnels within the enclosures. In time it was possible to locate anal marking sites visually as a result of discolouration of the marked object, as more and more layers of scent were deposited.

The anal drag was made by depressing the opened anal sac onto an object, as was described in Ewer (1973). The use of the handstand position as recorded by Hediger (1949) and Ewer (1973) was observed only three times during this study. On all occasions the mongoose concerned marked the upright walls of the nestbox after introduction to a new enclosure. The substance that was deposited had an oily consistency and was black when initially deposited. As time elapsed and the amount of secretion built up as a result of repeated marking activity, the deposit became creamy. On occasion the mongooses forcibly ejected anal fluid from the anal sacs, usually when startled or in stressful situations. This fluid was black, strong-smelling and extremely volatile. Initially the odour was overpowering, but over a period of 24 h it dissipated and was noticeable only if the deposit was closely investigated. After three days the smell was no longer distinguishable by the observer.

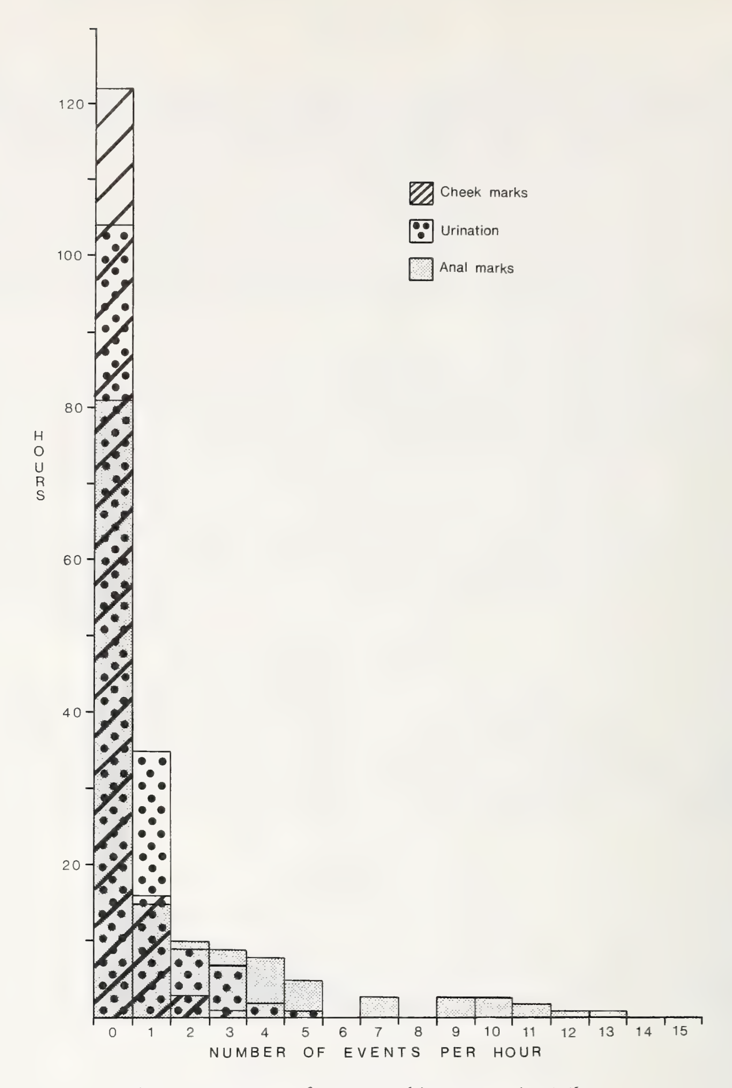


Fig. 1. Frequency of scent marking events in *Atilax*

Cheek rubbing

Cheek rubbing frequency varied from zero through three times per hour ($\bar{x} = 0.17$, n = 142). Frequency of cheek rubbing was significantly higher in the presence of known conspecifics (d = 2.89, $0.01 > p > 0.001$). During the breeding season females marked significantly more than during the non-breeding season (d = 3.31, $0.001 > p > 0.0001$), while in males no significant difference was found (d = 0.9, $p > 0.1$). The most commonly rubbed objects included the entrance to the nestbox, tree stumps and tunnels.

Cheek rubbing involved slowly wiping the sides of the head, from the corners of the mouth to the base of the ear pinnae, against an object. The secretion was never visible and the marked object bore no humanly-noticeable smell. However, the cheeks of the mongooses did have a pleasant honey-like odour. Figure 2 shows the sequences of behaviour patterns followed during glandular marking. Twelve transitions are shown,

indicating that the most common actions involved initially smelling the object to be marked, followed by either cheek or anal marking. The observed transition matrix was significantly different from a random distribution, $\chi^2 = 171.23$, d.f. = 16, $p < 0.001$. Mean duration of sequences was 11.61 sec, n = 40, SD = 9.72.

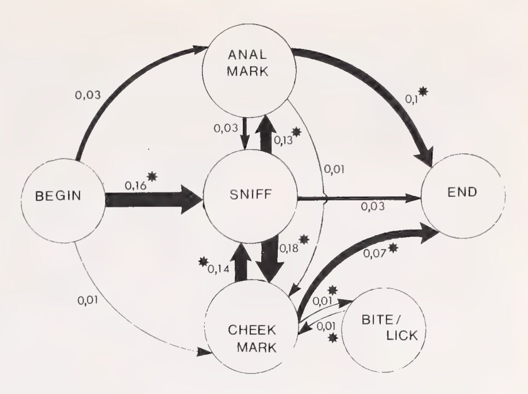


Fig. 2. Flow diagram showing the sequence of behavioural events during scent marking by *Atilax*. * Transitions above expected values

Discussion

The most frequent scent marking pattern used by *Atilax* is anal marking, followed by urination, cheek marking and then defaecation.

Clearly the amount of faecal and urinary material produced by a mongoose is dependent on its dietary intake. This may affect the frequency of defaecation and urination. In a captive environment, animals receive a constant and usually abundant supply of nutrients, so that the results reported here in respect of these two functions may bear little resemblance to the situation in naturally occurring *Atilax*. However, urination appears to serve not only as a means of excretion but also as a marking method. This is demonstrated by the high frequency of this activity, and the fact that only a few drops of fluid need be produced at a time.

The use of middens by carnivores is widespread (Macdonald 1980). While middens in this study were never located on rocks, middens in the field are regularly found on rocky outcrops and bare expanses of rock as well as on sandy river banks. The lack of rock use by captive animals probably resulted from the absence of suitably large rocky surfaces. In *Atilax* midden use may be the most efficient method of information dissemination, regarding the inhabitants of a particular area. If, as Ewer (1973) suggests, the faeces are coated with anal gland secretions as they pass out of the body, the scats become the calling card of that particular individual. Gorman (1976) has shown that individual *Herpestes auropunctatus* can recognize the anal gland secretions of particular conspecifics, and Hefetz et al. (1984) have shown that *Herpestes ichneumon* males produce an anal scent component that is specific to their sex. Rasa (1973) has also shown that dwarf mongoose scats bear the identity of the individual but that the identifying scent of faeces does not persist for long periods. If we are to assume that the same characteristics of faecal material apply to water mongooses then the importance of regular use of the same middens becomes apparent; by continuously using the same midden the scent of an animal is renewed regularly enough to inform other conspecifics of its presence.

The infrequent use recorded during this study of the handstand position in anal scent deposition may result from an insufficient number of appropriate upright marking posts. Further, as handstand marking was performed only when a mongoose was introduced to a new enclosure, it may be concluded that handstand marking is used only in those circumstances when the mongooses are highly motivated to mark.

Although cheek glands have not been anatomically described for this species, their presence is indicated on behavioural grounds both here and elsewhere (Zannier 1965; Rasa 1973).

The marking sequences show a clear relationship between cheek marking and sniffing. As cheek marking was usually (50.7 % of the time) preceded by sniffing, it seems that the mongooses initially ascertained the status of the previous mark before either renewing their

own or covering that of a conspecific. Most cheek marking behaviour (96 %) occurred when mongooses were housed with a conspecific of the opposite sex during the breeding season. During these times levels of agonistic behaviour were high and 71.4 % of the cheek marking episodes were carried out by females. If we assume that cheek marking carries a message of excitement/threat as in dwarf mongooses (RASA 1973), then the incidence of cheek marking during premating encounters is understandable, as during this period the female wards off and avoids the male. Only when she is ready to copulate does she cease cheek marking and entirely submit to her mate's demands.

In *Helogale* (RASA 1973) cheek marking is preceded by sniffing 71.2 % of the time, while anal marking is shown to mainly follow cheek marking. In *Atilax,* on the other hand, anal marking was preceded by sniffing 37.3 % of the time and never followed cheek marking. In addition *Atilax* preceded most marking sequences by sniffing (88 % of the time), indicating the importance of scent marking in their communication.

RASA (1973) has shown that cheek marks in *Helogale* have a brief effective period when compared with anal marks. In view of the sociability of dwarf mongooses, based on kinship and the concomitant need to maintain cohesion in the group, cheek marks may play a vital role in dissuading potential conspecific intruders from attempting to join the group, and it is therefore essential to precede most marking bouts with cheek marks. RASA (pers. comm.) indicates that cheek marking plays no role in establishing and maintaining rank within the family group.

For solitary *Atilax* a situation in which conspecifics would want to become part of a group does not arise, and hence cheek marking takes on a less significant role. However anal marking reaches far more significance when the need to advertise their identity to potential mates is considered. This is supported by the higher frequencies of anal marking when compared with cheek marking.

Interestingly, licking follows only anal marking in *Helogale* (RASA 1973) while in *Atilax* licking followed only cheek marking. RASA (1973) suggests that the mongooses occasionally lick anal secretions because of the general interest engendered by these secretions as well as their lack of threat connotation. In *Atilax* the cheek marks that were licked belonged to the owner and licking always immediately followed the cheek mark. In these cases licking may serve to reassure the mongoose of the intended threatening message.

When water mongooses were presented with a strong-smelling compound such as a deodorant or insecticide they frantically cheek-marked the object, rather than anal-marked it. In these circumstances (which are clearly unlikely to occur within the natural environment) cheek marking may have no threat connotation, and is more likely to be released by high excitation levels.

In general there was an even distribution of anal marking regardless of the presence of conspecifics, although 58 % of marking sequences occurred when conspecifics were present. Considering the identifying function of anal marking it is to be expected that in the natural environment it should occur more regularly as it would inform conspecifics of their presence.

The major sources of contact with conspecific water mongooses would be along feeding routes and at middens, and it is for this reason that anal scent is important as discussed earlier. To be able to establish the most recent visit to a midden by a conspecific would convey information regarding potential mates in the area. This is supported by the significant difference in marking frequency in females during the breeding season. In sociable mongooses the use of middens is likely to play a less crucial role with regard to breeding, as the members of the group are in constant contact anyway.

Stoats, like water mongooses, are solitary animals. ERLINGE et al. (1982) has shown that dominance in these mustelids is conveyed by increased marking levels and that subordinate animals attempt to avoid or escape from the dominant partner. Water mongooses exhibited similar behaviour patterns when housed in pairs during the breeding season, in that

initially the male was dominant and the female exhibited avoidance and escape reactions. As the female approached readiness to copulate the dominance relationship reverses and the female cheek-marked more frequently, initiated allogrooming and ceased avoidance behaviour. RASA (1973) has shown that dominance status is not related to marking frequency in *Helogale,* but rather that age and sex of mongooses reflect marking frequency.

In this study *Atilax* exhibited sexual dimorphism with regard to anal marking, with females marking significantly more frequently ($d = 6.97$, $p < 0.00001$). In *Helogale* the reverse situation occurs with males marking more frequently with the anal glands than females (RASA 1973), and it is suggested that this may simply reflect sexual behaviour differences. However, cheek marking exhibited no such dimorphism in *Atilax* ($d = 1.21$, $p > 0.1$). ERLINGE et al. (1982) shows that stoats show no consistent difference in marking patterns in males and females, and goes further to say that this is expected in view of their spacing pattern. Stoats are solitary mustelids in which resident males and females exclude members of their own sex from their territories. Because the spacing pattern of *Atilax* in the natural environment has not been reported, no direct relationship between marking and territoriality can be made. In addition it has been noted that to assess direct relationships between marking and territorial behaviour is of limited value (BARRETTE and MESSIER 1980) as marking may simply be a means of expressing social status and reproductive condition (BEKOFF and DIAMOND 1976) or of familiarizing an animal with its environment (EWER 1968).

As males showed no significant difference in marking patterns throughout the year, it is suggested that they were transitory with regard to territories, while females maintained loose territories and advertised their presence and condition by varying marking frequency. The fact that females anal-marked less frequently during the breeding season and cheek-marked more frequently at this time, indicates that their excitement levels increased. By virtue of the increased intensity of cheek marking in conjunction with anal marking, males could readily perceive the reproductive condition of females.

KOEHLER et al. (1980) suggested that in wolverines marking may serve as a mechanism of avoidance, and that this may be a general feature of many solitary animals. When *Atilax* pairs were housed together for extensive periods avoidance by both mongooses was initially observable, but after a few weeks the animals regularly inhabited the same nestbox. When active, however the tendency to avoid one another was evident until the onset of the breeding season.

Scent marking in animals is clearly an important mode of communication that is influenced not only by motivational and circumstantial cues but also by physiological ones. In *Atilax* the use of scent is essential, especially in view of its solitary mode of life. The results indicate that the function of scent varies, serving to promote avoidance when evidence of oestrous is absent and facilitating contact during the breeding season.

Acknowledgements

Thanks are extended to: Prof. J. MEESTER for supervising this project and critically reading the manuscript; Prof. G. MACLEAN for translating the summary; Prof. A. RASA for commenting on the manuscript; the Council for Scientific and Industrial Research and University of Natal Research Fund for financial assistance; ELEANOR RICHARDSON and GRAHAME HAYES for support and also for caring for the animals in my absence.

Zusammenfassung

Duftmarkierung bei gefangengehaltenen Sumpfichneumons (Atilax paludinosus)

Unterschiedliche Methoden der Duftmarkierung von *Atilax paludinosus* in Gefangenschaft werden beschrieben. Die vier beobachteten Markierungsweisen sind Koten, Harnen, anale Markierung und Reiben der Wangen. Am häufigsten fand die anale Markierung statt, die bei Weibchen außerhalb der Fortpflanzungszeit noch häufiger war. Ferner ergab sich bei analer Markierung ein Geschlechtsunterschied, denn Weibchen markierten öfter als Männchen. Die Häufigkeit der Markierung durch Wangenreiben nahm zu, wenn sich Tiere derselben Art zusammenfanden; während der Fortpflanzungszeit markierten Weibchen signifikant mehr. Die Häufigkeit der Kotabgabe stand mit der Nahrungsaufnahme in enger Verbindung; Harnen nahm signifikant zu, wenn Mangusten sich mit Artgenossen zusammenfanden. Die Bedeutung dieser verschiedenen Markierungsarten und -muster wird mit Bezug auf die Ökologie der einzellebenden *Atilax* diskutiert, und mit dem Verhalten der geselligen *Helogale* verglichen.

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Z. Säugetierkunde 53 (1988) 365–379

ISSN 0044-3468

Zur Anatomie des Gehörorganes der Seekuh (*Trichechus manatus* L.), (Mammalia: Sirenia)

Von M. S. Fischer

Eingang des Ms. 5. 8. 1987

Abstract

Contributions to the anatomy of the hearing organ of the seacow Trichechus manatus L. (Mammalia: Sirenia)

The anatomy of the soft parts of the hearing organ of *Trichechus manatus* L. is described. Two specimens have been dissected and in both cases the external auditory meatus ends in a blind pouch, which has no contact to the tympanic membrane. The latter is pushed outwards by the Manubrium mallei. The tympanic membrane consists of unusual dense connective tissue. A major peculiarity of the middle ear of *Trichechus* is the tympanic sac. Ventrally the tympanic cavity is bordered by a membraneous sac. It encloses the space between the basioccipital, basisphenoid, the pterygoid process and the tympanic ring. The tympanic sac is part of the tympanic cavity and covered on the inner side with a respiratory epithelium. The Eustachian tube is highly divergent from the condition found in other mammals. A comparison of the tympanic sac with the Eustachian sac of Procaviidae, Equidae and Tapiridae reveals no homology between these two structures. Cautious reflexions on the function of the tympanic sacs suggest, that they could be a kind of air-cushion which isolate the ear against the sirenian's own vocalization. The problem of directional hearing under water and sound conduction is briefly discussed and applied to the morphology of the manatee.

Einleitung

Unsere derzeitigen Kenntnisse über das Gehörorgan der Sirenia beschränken sich fast ausnahmslos auf die Anatomie der Hartteilstrukturen (Hyrtl 1845; Claudius 1867; Doran 1876; van Kampen 1905; Matthes 1912; van der Klauuw 1931; Werner 1960; Robineau 1965, 1969; Fleischer 1971, 1973, 1976, 1978) und deren Ontogenese (Dilg 1909; Freund 1908; Matthes 1921; Hirschfelder 1936). Die umfassendste Darstellung der Skelettstrukturen findet sich in den Arbeiten von Robineau.

Das Problem des Hörens bei aquatischen Säugetieren hat in den letzten Jahrzehnten großes Interesse erregt, und es sind wichtige Arbeiten hierzu veröffentlicht worden, die zumeist die Anatomie und Hörphysiologie der Wale betreffen (z. B. Reysenbach de Haan 1957; Repenning 1972; Purves und Pilleri 1983). Der Weichteilanatomie des Ohres der Seekühe ist hingegen keine Aufmerksamkeit zuteil geworden. Leider sind in Arbeiten von Fleischer (1971–1978) die anatomischen Verhältnisse nur schematisch wiedergegeben. Da kürzlich neue Befunde über das Hörvermögen der Seekühe bekannt geworden sind (Bullock et al. 1982), die die Möglichkeit des Ultraschallhörens auch bei dieser aquatischen Gruppe in Betracht ziehen, erschien eine anatomische Untersuchung des Gehörorganes der Seekühe umso wünschenswerter.

Die Kenntnis der Anatomie der Weichteile dieser Region ist in einem weiteren Zusammenhang von Bedeutung. Dem Auftreten von Diverticula tubae Eustachii kommt möglicherweise ein besonderer Wert für die Systematik der Perissodactyla (Mesaxonia + Hyracoidea) zu (Fischer 1986). Da Murie (1874) einen „Eustachian sac" bei *Trichechus manatus* beschrieb und bekanntlich von vielen Autoren eine enge Verwandtschaft zwischen Sirenia, Proboscidea und Hyracoidea angenommen wird, muß somit auch geklärt werden, inwieweit eine Homologie zwischen den Luftsäcken der Perissodactyla und der Sirenia besteht.

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In der vorliegenden Arbeit will ich eine ausführliche Beschreibung der Anatomie des Mittelohres und insbesondere des Tympanalsackes von *Trichechus manatus* geben, und die Befunde mit den Verhältnissen der Cetacea und Perissodactyla vergleichen. Darüber hinaus soll versucht werden, Besonderheiten des Gehörorganes der Seekühe auf die Bedingungen des Hörens unter Wasser zu beziehen.

Material und Methode

Die Sektion wurde an einem Exemplar der Seekuh *Trichechus manatus* L. durchgeführt, die Prof. Starck für die Sammlung der Senckenbergischen Anatomie 1975 vom Zoologischen Garten Duisburg erhalten hatte. Das Alter des Tieres ist unbekannt, da es sich um einen Wildfang aus Guyana handelte.

Abmessungen: Gesamtlänge (Schnauzenspitze – Schwanzflossenspitze) = 158 cm, Länge Schnauzenspitze – Analöffnung = 103 cm, Länge Schnauzenspitze – äußere Gehörgangsöffnung = 22,5 cm, Leibesumfang in Höhe des Nabels = 107 cm.

Das Tier wurde über die Schwanzarterie mit 4 %igem Formalin perfundiert und in 4 %igem Formalin aufbewahrt. Die makroskopische Präparation wurde durch histologische Untersuchungen des Tympanalsackes, des Trommelfelles, des Endabschnittes des äußeren Gehörganges und verschiedener Abschnitte der Tuba Eustachii ergänzt. Der Erhaltungszustand der Gewebe war nicht immer befriedigend.

An einem juvenilen Tier, welches die zoologische Schausammlung der Universität Tübingen kurz vor Abschluß der Arbeit aus Florida erhielt, wurde eine Kontrollsektion des äußeren Gehörganges durchgeführt.

Ergebnisse

Meatus acusticus externus

Die winzige äußere Ohröffnung (Abb. 1), durch die, wie schon Murie (1874) bemerkte, gerade eine Sonde eingeführt werden kann, liegt 11 cm hinter dem Auge. Der Gehörgang (Meatus acusticus externus) durchbricht die an dieser Stelle 14 mm dicke Haut und nimmt

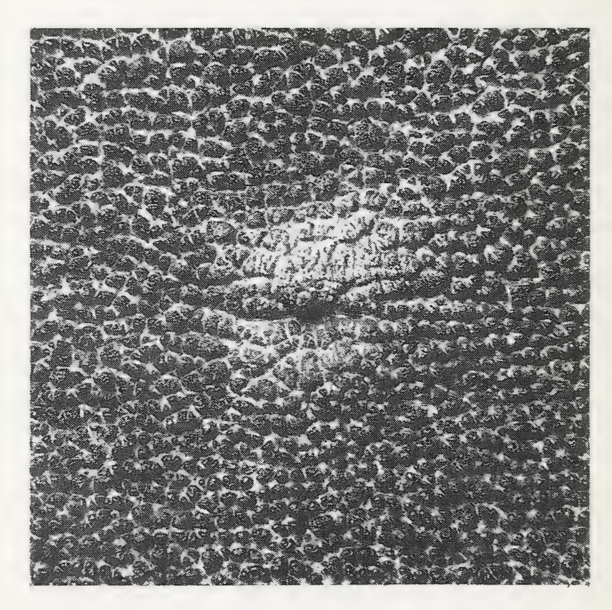


Abb. 1. Die äußere Ohröffnung von *Trichechus manatus.* Die äußere Ohröffnung ist von der sie umgebenden Haut nur durch die hellere Färbung zu unterscheiden

einen caudoventralen Verlauf. Er erweitert sich zu einem Sack, der überraschenderweise blind endet (Abb. 2). Der Blindsack hat keinen Kontakt zum Trommelfell. Die Länge des äußeren Gehörganges ist 53 mm. Der Durchmesser des Blindsacklumens beträgt maximal 5 mm und ist damit etwa doppelt so groß wie das Lumen des Gehörganges. Aus dem medialen Teil der äußersten bindegewebigen Umhüllung des Meatus acusticus externus

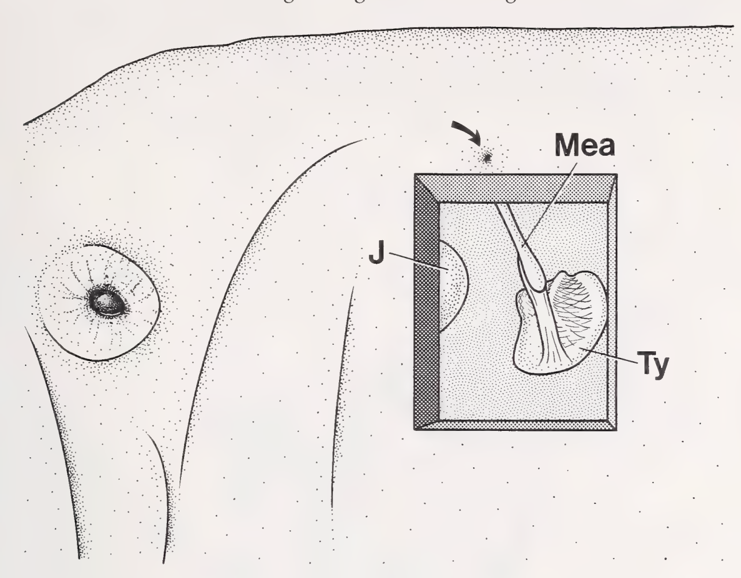


Abb. 2. Trichechus manatus. Die Zeichnung zeigt die Lage des äußeren Gehörganges (Mea). Er durchbricht zunächst die dicke Haut und endet in Höhe des Jochbogens (J) in einem Blindsack, der keine Verbindung zum Trommelfell besitzt. Die Ohröffnung (Porus acusticus) ist durch einen Pfeil markiert

geht ein Band hervor, das den Unterrand des Blindsackes fixiert, sich flächenartig verbreitert und am ventralen Rand des Tympanicum ansetzt. Dieser Befund konnte an dem erwähnten juvenilen Exemplar von *Trichechus manatus* der Zoologischen Schausammlung der Universität Tübingen überprüft werden. Auch bei diesem Exemplar endete der äußere Gehörgang in einem Blindsack. Dies steht im Widerspruch zu der Beobachtung von Murie (1874), der einzigen, die ich in der Literatur gefunden habe. Er beschreibt den äußeren Gehörgang als „a narrow cord-like fibrous tube, 3 inches long, with an S-shaped bend, leads to the membrana tympani" (Murie 1874, p. 188). Ob der äußere Gehörgang bei den Seekühen eine Funktion beim Hören hat, scheint sehr fraglich zu sein.

An der Lumenseite ist der äußere Gehörgang mit einer dunklen, stark pigmentierten Schicht ausgekleidet. Die histologische Untersuchung zeigt, daß es sich um ein unverhorntes mehrschichtiges Plattenepithel handelt, und daß die Pigmentzellen in den unteren Epithelschichten liegen. Des weiteren sieht man im Querschnitt mehrere Lagen konzentrisch angeordneter, abwechselnd longitudinal und circulär ziehender Bindegewebsfasern. Es finden sich keine Drüsen. Die mirkoskopische Untersuchung bestätigt auch, daß der Meatus acusticus externus in der Tiefe allmählich sein Lumen verliert und blind endet.

Membrana tympani

Schon lange ist bekannt, daß das Trommelfell der Seekühe, verglichen mit anderen Säugetieren, eine einzigartige Form besitzt. Es wird vom Manubrium mallei, das dabei die Form eines leicht nach rostral gekippten Ringes hat, zeltartig nach lateral vorgebuchtet

(Abb. 3, 4). Das Trommelfell ist in einem seichten Sulcus tympanicus befestigt. Dorsal des Manubrium mallei schlägt es nach innen um und inseriert am Innenrand des Malleus. Oberhalb des vorderen Schenkels des Tympanicum dehnt sich das Trommelfell rostrad aus. Auch dieser Teil des Trommelfelles wendet sich scharf nach innen um. Er ist an der medialen Seite des Caput mallei befestigt. Die Grenze zwischen dem gespannten und dem schlaffen Teil des Trommelfelles verläuft vom höchsten Punkt des vorderen Schenkels schräg nach dorsal. Sie ist als weiße Linie in Abb. 3 eingezeichnet. Ob dieser schlaffere Teil des Trommelfelles der Pars flaccida (Shrapnellsche Membran) entspricht, wie Robineau (1969) annimmt, kann hier nicht entschieden werden.

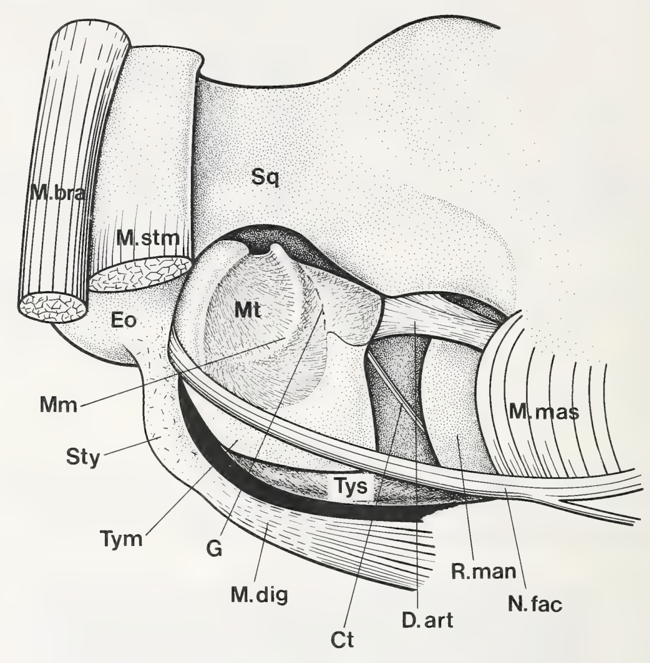


Abb. 3. Trichechus manatus. Lateralansicht der Tympanalregion. Das in dem hufeisenförmigen Anulus tympanicus aufgespannte, derbe Trommelfell wird vom Manubrium mallei (Mm) nach außen gedrückt (vgl. Abb. 4). Der kräftige N. facialis (N. fac) verläßt das Cavum tympani zwischen Anulus tympanicus und dem knorpeligen Teil des Stylohyale (Sty). Ventral des Trommelfellringes erkennt man den lateralen Teil des Tympanalsack

Der Durchmesser des straff gespannten Trommelfelles beträgt in caudorostraler Richtung 19 mm und dorsoventral 24 mm. Fleischer (1971) gibt den Durchmesser bei 2 Exemplaren von *Dugong dugon* mit 16 mm und 19 mm an. Nach Fleischer (1978) beträgt der Durchmesser des Trommelfelles der Sirenia durchschnittlich 20 mm. Der Dünnschnitt ergibt eine Dicke des Trommelfelles von 0,6 mm.

Die histologische Untersuchung zeigt, daß das Trommelfell von einer ungewöhnlich derben, wohlgeschichteten Bindegewebsplatte gebildet wird. Das Bindegewebe zeigt geordnete längs- und querverlaufende Züge, die auf eine sehr starke Verflechtung schließen lassen. Unterhalb des mehrreihigen Epithels, das das Trommelfell zum Cavum tympani hin bedeckt, finden sich wenige muköse und seröse Drüsen. Ein äußeres Epithel ist wegen der fehlenden Verbindung mit dem äußeren Gehörgang nicht mehr vorhanden. Dem Trommelfell schließt sich hier ein lockeres Bindegewebe mit elastischen Elementen an.

Hyrtl (1845) und Doran (1876) beschreiben, daß das Trommelfell bei *Dugong dugon* nicht wie bei *Trichechus* durch das Manubrium mallei lateral vorgestülpt, sondern plan sei.

Hydrodamalis gigas stimme dagegen mit den Verhältnissen bei *Trichechus* überein. Die Beobachtung an 9 Schädeln aus den drei Gattungen der Sirenia mit den Gehörknöchelchen in situ, die ich im British Museum (Natural History) untersuchte, legt die Vermutung nahe, daß der Malleus durch die Mazeration seine distale Verbindung zum Anulus tympanicus verliert. Infolge des Verlustes dieser Befestigung könnte der Malleus durch die Spannung des Trommelfelles in die Paukenhöhle zurückgedrängt werden. So ist möglicherweise der beoboachtete Unterschied zwischen *Dugong* und *Trichechus* auf ein Mazerationsartefakt zurückzuführen. Es sei auch noch bemerkt, daß das von Fleischer (1971) beobachtete Knochenplättchen am rostroventralen Rand des Anulus tympanicus bei den von mir untersuchten Exemplaren nicht auftrat.

Tympanalsack

Bei den Sirenia wird medial des Anulus tympanicus der Boden der Paukenhöhle von einem membranösen Sack gebildet. Da dieser Sack und die Paukenhöhle offen miteinander kommunizieren und von der selben Schleimhaut ausgekleidet werden, ist davon auszugehen, daß es sich um eine Vergrößerung des Cavum tympani handelt.

In der Literatur finden sich nur zwei kurzgefaßte Bemerkungen von Murie (1874) und Robineau (1965) über den Tympanalsack. Sie beschränken sich darauf seine Lage zwischen Basisphenoid, Basioccipitale, Exoccipitale und Tympanicum zu beschreiben. Eine von Fischer (1986) wiedergegebene briefliche Mitteilung von D. P. Donning enthält die zusätzliche Information, daß der Tympanalsack in Höhe des Processus pterygoideus in die ziemlich große Tuba Eustachii übergehe.

Die Tympanalsackmembran löst sich medial vom Anulus tympanicus ab (Abb. 3, 4), der so die laterale Begrenzung des Tympanalsackes bildet. Caudal liegt der Tympanalsack dem knorpeligen Beginn des Zungenbeines an. Vom M. brachiocephalicus bedeckt, zieht er zu den Austrittsstellen der Hirnnerven IX–XII, auf deren Höhe sich die Membran scharf nach rostral wendet und eine Duplikatur bildet, die die A. carotis interna und den N. caroticus internus vom Eintritt in den Tympanalsackraum bis zum Übergang in den Schädel umgibt. In Abb. 4 und Abb. 6 ist die Richtung der Duplikatur (Dupl.) wiedergegeben. Im Anschluß an diese Faltenbildung verläuft die Grenze des Tympanalsackes entlang des lateralen Randes der Schädelbasisknochen Basioccipitale und Basisphenoid und um die Insertion des M. longus capitis und des M. rectus capitis ventralis herum. Unmittelbar rostral der Ansatzstelle dieser beiden Kopfbeuger berühren sich die Tympanalsäcke der rechten und linken Seite in der Medianebene. Rostroventral stoßen sie an den Bindgewebsblock, der den pharyngealen Abschnitt der Tuba Eustachii umgibt. Rostrolateral liegt der M. tensor veli palatini der Tympanalsackwand an. Die dorsale Wand des Tympanalraumes ist zugleich die ventrale Abdeckung der Fissura sphenopetrose (Foramen lacerum medium). Die Tympanalsackmembran ist zwischen der Schädelbasis und dem Petrosum ausgespannt. Die in Abb. 4 eingezeichnete Schnittebene (S) zeigt, daß der Mediosagittalschnitt (Abb. 5) den Tympanalsack geringfügig parasagittal getroffen hat, so daß man ihn im Anschnitt sieht. In Höhe ihrer Berührungsflächen befinden sich die Tympanalsäcke ventral des Tuberculum musculare an der Synchondrosis sphenooccipitalis. Der Ventralseite des Tympanalsackes liegt ein kräftiger Fettkörper an, der sich auch zwischen seine Wand und den M. stylopharyngeus einschiebt. Er wurde in Abb. 5 nicht eingezeichnet, um die Eintrittstelle der A. carotis interna und des N. caroticus internus in die ventrale Tympanalsackwand darzustellen.

Nach Öffnung des Tympanalsackes auf der Ventralseite (Abb. 6) sieht man, daß der Tympanalsackraum durch zwei sich gegenüberstehende sichelförmige Falten, die eine elliptische Öffnung freilassen, in zwei Kompartimente unterteilt wird. Die beiden Falten (v. F. + h. F.) liegen in der Verlaufsrichtung der Tuba Eustachii und können am Schädel als caudale Fortsetzung der Kante gedacht werden, die selbst als auslaufende Lamina medialis

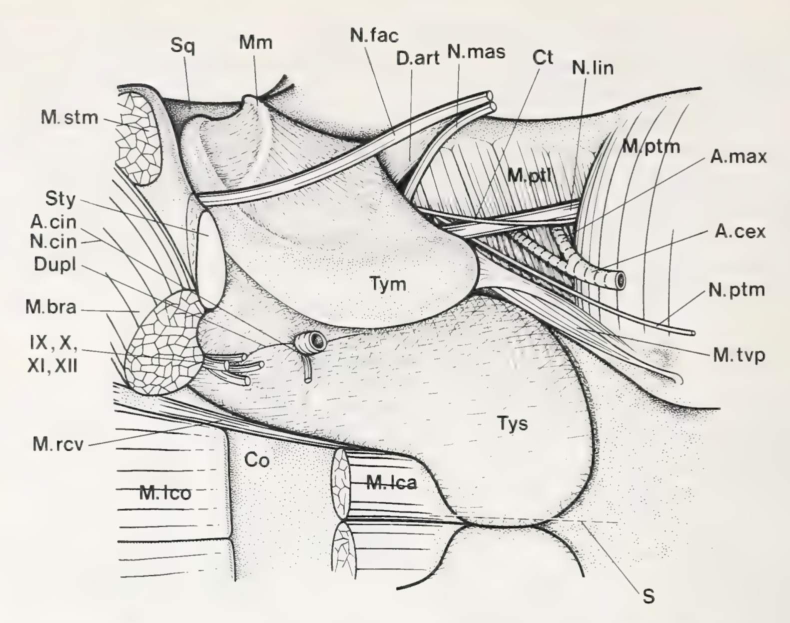


Abb. 4. Trichechus manatus. Die Präparation der Ventralseite der Region zwischen Tympanicum und Schädelbasis zeigt die Größe der Tympanalsäcke. Sie berühren sich in der Medianebene. Ausgehend von den Hirnnerven IX–XII ist die Duplikaturfalte eingezeichnet, in welche die A. carotis interna eingehüllt ist. Die Duplikatur unterteilt den von den Tympanalsackmembran umschlossenen Raum. Die gestrichelte Linie markiert die leicht parasagittale Schnittführung der in Abb. 5 gegebenen Ansicht

proc. pterygoidei aufzufassen ist. Die hintere Falte ergibt sich aus der beschriebenen Duplikatur der caudalen Tympanalsackmembran. Sie endet rostral 1–2 cm vor der Eintrittsstelle der A. carotis interna (Abb. 6). Zwischen der hinteren Falte und dem rostralen Rande des Anulus tympanicus bleibt ein spaltförmiger, hoher Durchtritt zum lateralen Tympanalsackraum und demjenigen zwischen Tympanicum und Petrosum. Ob hier ein Verschluß in der Art eines Klappenventiles des medialen gegen den lateralen Raum vorgenommen werden kann, ist am toten Tier nicht zu klären.

Caudal der A. stapedialis finden sich Ausbuchtungen in dem Teil der Tympanalsackmembran, der vom ventrocaudalen Rand des Petrosum ausgeht und die laterale Wand der Duplikatur bildet, die die A. carotis interna und A. stapedialis umhüllt (Abb. 6). Es treten 3 größere und 5 kleine Ausbuchtungen (Cellulae tympanicae?) auf. Im Anschluß an die am weitesten dorsocaudal gelegene Ausbuchtung bildet das Cavum tympani eine tiefe Aushöhlung zwischen Petrosum und Exoccipitale. Auch rostral findet sich eine geräumige membranöse Ausbuchtung zwischen Petrosum und der Ventromedialseite des Anulus tympanicus. D. P. Domning beobachtete bei zwei Exemplaren von *Trichechus inunguis* keine Ausbuchtungen im caudalen Abschnitt (Domning briefl. Mittl. v. 19. 6. 1987).

Trotz der für histologische Untersuchungen mangelhaften Erhaltung des Präparates erkennt man auf dem mikroskopischen Präparat noch vereinzelt Kinocilien an dem mehrreihigen, mit wenigen Becherzellen besetzten Epithel, das den Tympanalsack auskleidet. Dieses respiratorische Epithel wird von einer drüsen-, gefäß- und nervenreichen Lamina propria unterlagert. Die Zahl der mukösen und serösen Drüsen ist im Bereich des Anulus tympanicus deutlich geringer als in der Schleimhaut der Tympanalsackmembran des beschriebenen Nebenraumes. Die Membran besteht im weiteren aus einem unregelmäßigen, straffen Bindegewebe mit wechselnder Schichtung. Die Dicke der gesamten Membran beträgt 0,4–0,5 mm.

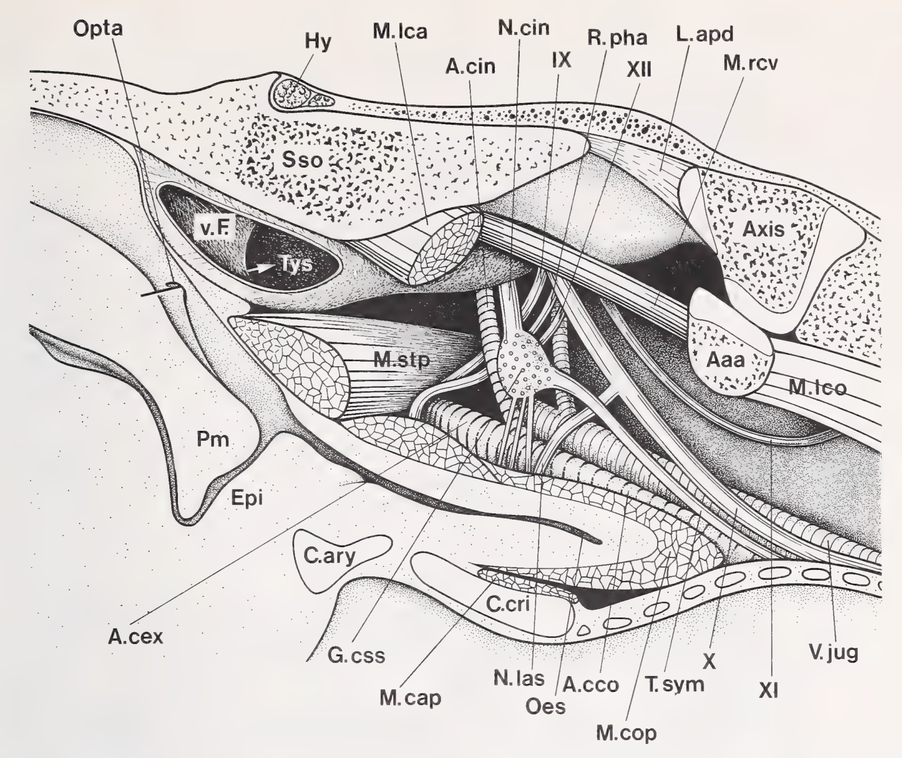


Abb. 5. Trichechus manatus. Der Mediosagittalschnitt zeigt die Lage des Tympanalsackes (Tys) zwischen wirbelseitiger Rachenwand, Schädelbasis und M. stylopharyngeus (M. stp). Der M. longus capitis (M. lca) ist am Ansatz abgeschnitten. Die Tuba Eustachii (Pfeil) öffnet sich nach nur kurzem Verlauf in den Tympanalsack, lateral einer vorderen Falte (v. F.). Deutlich ist die Aufspaltung der A. carotis communis (A. cco) zu sehen und der Eintritt der A. carotis interna (A. cin) in die ventrale Wand des Tympanalsackes. Man beachte die ungewöhnliche Form der Epiglottis

Cavum tympani

Da der Tympanalsack und die knöchernen Anteile des Cavum tympani von derselben Schleimhaut ausgekleidet werden und der vom Tympanalsack umgebene Raum eindeutig zur Paukenhöhle gehört, entsteht eine Gliederung des Cavum tympani in mehrere Kompartimente. In der Reihenfolge von medial nach lateral sind dies zunächst der medial der vorderen und hinteren Falte liegende Teil des Tympanalsackraumes. Daran schließt sich der durch die Faltenbildungen charakterisierte laterale Tympanalsackraum an, der sich rostral in die Tuba Eustachii fortsetzt. Auf das Problem der Abgrenzung der Tuba Eustachii vom Mittelohrraum wird weiter unten eingegangen. Die beiden Tympanalsackräume könnten in Anlehnung an van Kampen (1905) hypotympanale Nebenhöhlen genannt werden. Der laterale Tympanalsackraum geht in den Raum über, der zwischen Anulus tympanicus und Trommelfell, Tegmen tympani und Petrosum liegt und den man nach van Kampen als Paukenhöhle im engeren Sinne bezeichnet. Zu dieser gehört auch der sich unter dem kuppelförmigen Tegmen tympani ausbreitende große Recessus epitympanicus.

Tuba Eustachii

Über die Tuba Eustachii der Sirenia finden sich nur zwei kurze Angaben in der Literatur. „The large Eustachian tube communicates with the auditory chamber just in front of the

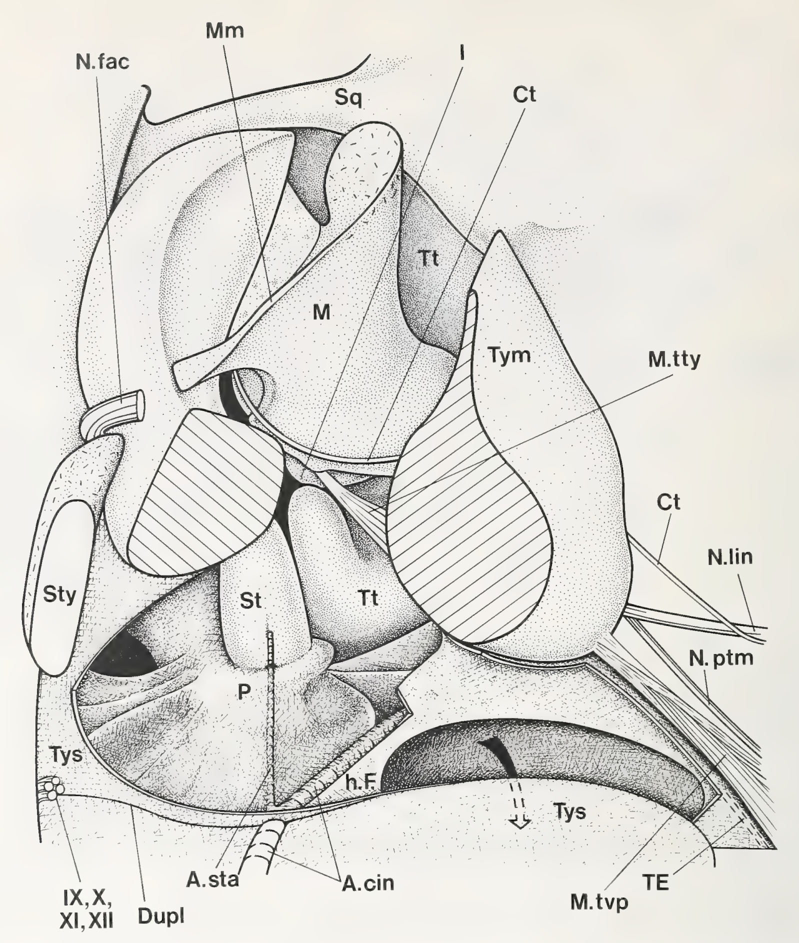


Abb. 6. Trichechus manatus. Ventrolateralansicht der Mittelohrregion. Das Trommelfell und ein Teil des Anulus tympanicus wurden entfernt. In die ventrale Tympanalsackmembran wurde ein großes Fenster geschnitten. Die innere Schleimhaut des Tympanalsackes geht ohne makroskopisch oder histologisch erkennbare Veränderung aus der das Cavum tympani auskleidenden Schleimhaut hervor. An den Gehörknöcheln und am Tegmen tympani (Tt) wurde die Schleimhaut nicht eingezeichnet. Die erwähnte Duplikatur der Tympanalsackmembran bildet eine hintere Falte (h. F.), die zum Petrosum (P) zieht und in z. T. tiefe membranöse Kammern unterteilt ist. Durch eine elliptische Öffnung stehen die beiden von der Tympanalsackmembran umschlossenen, hypotympanalen Räume in Verbindung (Pfeil). Man beachte auch die dünne A. stapedialis (A. sta) und die ungewöhnliche Form des Malleus

stylo – hyal cartilage" (Murie 1874, p. 188); und „grossièrement piriforme, l'oreille moyenne des Siréniens se rétrécit progressivement vers l'avant et vers l'intérieur et se conduit par la trompe d'Eustache, étroit conduit fibreux qui suit le bord postérieur de l'aile interne de l'apophyse pterygoïde, puis s'en écarte vers l'intérieur pour déboucher dans le pharynx" (Robineau 1965, p. 413).

Der pharyngeale Tubeneingang (Abb. 5) zeigt keine Besonderheiten. Das Lumen der Tuba Eustachii ist sehr weit und eigentlich mit dem Begriff „Röhre" unzureichend charakterisiert. Das Lumen hat vielmehr am etwas über 1 cm langen Abschnitt am pharynxseitigen Anfangsteil der Tuba Eustachii die Form einer hohen Spalte (Abb. 6). Bereits die in Höhe der rostralen sichelförmigen Falte vorhandene Mündung könnte als eigentliche funktionelle Öffnung der Tuba Eustachii in den tympanalen Raum angesehen

werden. Morphologisch ist keine eindeutige Entscheidung möglich, wo die Tuba Eustachii endet und die hypotympanale Nebenhöhle des Cavum tympani beginnt.

Um die Verhältnisse weiter zu klären, wurden histologische Schnitte von verschiedenen Abschnitten des tubotympanalen Raumes zwischen Pharynx und Mittelohr angefertigt. Dabei bestätigte sich, daß die Tuba Eustachii von *Trichechus* sehr stark von den üblichen Verhältnissen der Säugetiere abweicht. Schon in dem beschriebenen, kurzen, pharyngealen Anfangsteil der Tube fehlt ein typischer Tubenknorpel. Im Querschnitt finden sich nur einzelne Knorpelinseln inmittel des sehr kräftigen Bindegewebes. Drüsen treten nur im Bereich der ventralen Biegung auf. Die Lamina propria ist deutlich abgegrenzt. Drei schwache Muskelbündel, die nicht näher identifiziert werden konnten, ziehen an der Lateralseite entlang. Der Knorpel verschwindet nach ungefähr einem Drittel der Strecke zwischen Ostium pharyngeum tubae auditivae und Tympanicum. Im Anschluß bildet dichtes, von respiratorischem Epithel überzogenes Bindegewebe eine ventral zum Tympanalsack geöffnete, breite, V-förmige Rinne (Abb. 6). Medial des inneren Schenkels der Rinne liegen zahlreiche, tief ins straffe Bindegewebe der Lamina propria eingesenkte tubulo-muköse Drüsen, die verzweigt sind und einen weitlumigen Ausführgang besitzen. Wenige seröse Drüsen befinden sich an der Medialseite des inneren Schenkels.

Der M. tensor veli palatini entspringt an der Medialseite eines kräftigen Bandes, das, sich stetig verjüngend, vom rostralen Rand des Anulus tympanicus zum Processus pterygoideus zieht (Abb. 4, 6). Der schlanke Muskel umschlingt den Hamulus pterygoideus und strahlt mit einer sich fächerförmig verbreiternden Endsehne ventrolateral des Ostium pharyngeum tubae auditivae in den weichen Gaumen ein. Der Muskel hat keine erkennbaren Beziehungen zur Tuba Eustachii. Er wird von Ästen aus dem lateral vorbeiziehenden N. pterygoideus medialis innerviert. Nach Werner (1960) ist ein auf das Tympanicum verlagerter Ursprung des Muskels ein sekundärer Zustand. Bei den von Domning (1977, 1978) untersuchten Seekühen entspringt der M. tensor veli palatini mit einer breiten flachen Sehne vom Anulus tympanicus und von der Fossa pterygoidea.

Die Muskeln der Gehörknöchelchen

Bestätigen kann ich die Beschreibung des M. tensor tympani und des M. stapedius von Domning (1978). Der M. tensor tympani entspringt an einem Vorsprung an der caudalen Basis des Processus pterygoideus. Er unterquert die Knochenbrücke zwischen Anulus tympanicus und Tegmen tympani und inseriert mit einer kurzen, kräftigen Endsehne am Processus muscularis mallei (Abb. 6). Robineau (1964 zit. in Saban 1968) beschreibt den Muskel als „dégénèré en tissu fibreux chez les Siréniens". In einer späteren Arbeit bildet Robineau (1969) den M. tensor tympani als gut ausgebildeten Muskelbauch ab, gibt aber keine Beschreibung.

Der M. stapedius ist ein fächerförmiger Muskel, der in einer Grube entspringt, die caudomedial des Sulcus nervi facialis liegt und von Robineau (1969) und Domning (1978) als Fossa muscularis minor des Perioticum bezeichnet wird. Er legt sich dem ihn innervierenden N. facialis ventral eng an. Mit einer kurzen Endsehne inseriert er an einem kleinen Vorsprung am Caput des Stapes.

Arteria carotis interna und Arteria stapedialis

Die A. carotis interna gibt unmittelbar nach Eintritt in die Duplikatur der Tympanalsackwand die A. stapedialis ab (Abb. 6). Erstere verläuft an der Medialseite der hinteren sichelförmigen Falte zum Foramen lacerum medium, wo das Gefäß zusammen mit dem N. caroticus internus in die Schädelhöhle eintritt. Die A. stapedialis liegt dem Promontorium auf und zieht zum Stapes, wo sie durch das sehr enge Foramen intercrurale hindurchgeht. Der Austritt aus dem For. intercrurale des ohnehin schwachen Gefäßes ist nicht mehr mit

Sicherheit nachzuweisen. Es kann nicht ausgeschlossen werden, daß es sich um ein nutritives Gefäß für den Stapes oder die ihn umgebende Schleimhaut handelt. Eine übereinstimmende Beschreibung der Verhältnisse dieser beiden Gefäße bei *Dugong dugon* findet sich bei Robineau (1969).

N. facialis und Chorda tympani

Der N. facialis nimmt bei *Trichechus manatus* denselben Verlauf wie bei *Dugong dugon* (Robineau 1969). Dem sehr kräftigen N. facialis legt sich im Hirnraum ein dünner Nerv an, bei dem es sich vermutlich um den N. intermedius handelt. Die ungewöhnliche Stärke des N. facialis hängt sicher mit der wohlausgebildeten mimischen Muskulatur, besonders der Schnauzenregion, zusammen. Auffallender Weise tritt der Nerv aus dem Cavum cranii nicht durch einen verknöcherten primären Faciliskanal aus, sondern durch eine, am mazerierten Schädel gut sichtbare tiefe Incisur zwischen dem oralen Pol des Petrosum und dem Tegmen tympani. Es tritt somit keine verknöcherte Commissura suprafacialis auf. Hingegen ist bei Seekuhfoeten diese Commissur vorhanden (Freund 1908; Matthes 1921; Hirschfelder 1936). Da der N. petrosus major lateral dieser Commissur abgeht, wird sie von Matthes (1921) mit der inneren Facialiscommissur homologisiert. Eine Commissura suprafacialis lateralis tritt diesem Autor zufolge bei den Sirenia nicht auf. Während des Verlaufes in der medialen Wand der Paukenhöhle bleibt der N. facialis jederzeit frei sichtbar; es kommt somit nicht zur Ausbildung einer zweiten Abteilung des Facialiskanales (van Kampen 1905). Nur anfänglich verläuft der Nerv in einem seichten Sulcus facialis, der auch bei foetalen Exemplaren beschrieben wird (Freund 1908; Hirschfelder 1936). Lateral der Articulatio incudostapedia und des M. stapedius zieht der Nerv zur Unterseite der knöchernen Verbindung zwischen Tympanicum und Petrosum. Der N. facialis verläßt die Paukenhöhle durch eine Öffnung (For. stylomastoideum primitivum), die ventral und caudal vom Anfangsteil des Zungenbeines, dorsal vom Processus posttympanicus und rostral vom Tympanicum begrenzt wird (Abb. 3, 4, 6).

Nach Austritt aus dem Cavum tympani gibt der N. facialis die Chorda tympani ab. Durch einen kleinen Kanal im hinteren Schenkel des Tympanicum gelangt sie in die Paukenhöhle zurück. Im weiteren verläuft sie medial der Basis des Manubrium mallei (Abb. 6). Sie steht in keiner Beziehung zur Articulatio incudomallearis, und so muß der von Fleischer (1971) beobachtete Kanal in diesem Gelenk, den er fragend in Verbindung mit der Chorda tympani bringt, einem anderen Zwecke dienen. Lateral und dorsal des Ansatzes des M. tensor tympani zieht die Corda tympani am Corpus mallei entlang und verläßt dorsal der breiten vorderen Knochenbrücke zwischen Tympanicum und Tegmen tympani (Fissura petrotympanica) das Cavum tympani. Robineau (1969) weicht in seiner Beschreibung der Verhältnisse der Chorda tympani bei *Dugong dugon* insoweit ab, als er proximal keinen Durchtritt durch einen besonderen Kanal und einen kurzen Verlauf der Chorda tympani auf dem Incus und auf dem M. tensor tympani beobachtete.

Der mit dem Tympanicum verbundene Anfangsteil des Zungenbeines entspricht dem Tympanohyale (van Kampen 1905; Robineau 1969). Bei dem mir vorliegenden Exemplar verbindet sich das Zungenbein mit der erwähnten Knochenbrücke zwischen Tympanicum und Petrosum, dem angrenzenden Processus posttympanicus und dem Exoccipitale. van Kampen (1905) erwähnt nur die erste und letzte Verbindung. Das Zungenbein ist somit opisthotrematisch (Howes 1896).

Diskussion

Zunächst soll die eingangs gestellte Frage nach der möglichen Homologie der Tympanalsäcke der Trichechidae mit den Luftsäcken der Procaviidae, Equidae und Tapiridae diskutiert werden. Fischer (1986) hat die Morphologie der Luftsäcke (Diverticula tubae

Eustachii) der Schliefer und Pferde beschrieben und mit derjenigen der Tapire verglichen. Bei diesen drei Gruppen stülpt sich der mittlere Abschnitt der häutigen Tube ventral zu voluminösen, luftgefüllten Säcken aus. Diese Tubendivertikel sind grobtopographisch mit dem Tympanalsack der Trichechidae vergleichbar. Während jedoch der Tympanalsack von *Trichechus* eine ventrale Erweiterung des Cavum tympani ist, wird bei den Procaviidae, Equidae und Tapiridae der membranöse Teil der Tuba Eustachii dilatiert. Die Tuba Eustachii ist hier sowohl an ihrem pharyngealen Anfangsteil als auch am tympanalen Endstück vor dem Eintritt in die knöcherne Bulla tympanica geschlossen. Auch der Verlauf der A. carotis interna ist bei den Procaviidae, Equidae und Tapiridae und den Trichechidae unterschiedlich. Während die Arterie bei den drei erstgenannten Gruppen auf der Medialseite des Luftsackes verläuft, durchquert sie bei *Trichechus* den ventralen Abschnitt des Cavum tympani. Bei dem Tympanalsack der Trichechidae und den Tubendivertikeln der Unpaarhufer und Schliefer handelt es sich dabei nach dem derzeitigen Stand unserer Kenntnis nicht um homologe Strukturen. Eine endgültige Klärung setzt jedoch auch hier ontogenetische Untersuchungen voraus. Die Befunde an *Trichechus* sprechen nicht gegen die von Fischer (1986) getroffene Annahme, die Luftsäcke als Synapomorphie der Hyracoidea und Mesaxonia anzusehen. Ob der Tympanalsack der Seekühe ein Primitivmerkmal ist, wie Robineau (1969) annimmt, scheint fraglich, da, wie eigene Befunde an *Elephas indicus* zeigen, die Tuba Eustachii der Elefanten eine geschlossene Röhre ist. So kann nicht eindeutig entschieden werden, welche Verhältnisse für den Grundplan der Tethytheria (Sirenia + Proboscidea) anzunehmen sind. Wie im folgenden ausgeführt wird, sind funktionelle Erklärungen denkbar, die den Tympanalsack als spezielle Anpassung an das Hören unter Wasser verständlich machen könnten.

Aussagen über die Funktion der Tympanalsäcke sind mangels experimenteller Daten nur in Analogie zu den Verhältnissen bei anderen aquatischen Gruppen möglich, obwohl die Topographie der Tympanalsäcke bei den Cetacea verschieden von derjenigen der Sirenia ist. Die in größerer Zahl auftretenden Tympanalsäcke („air-sacs", „sinuses") der Cetacea umgeben im Gegensatz zu den Verhältnissen bei *Trichechus* nahezu das gesamte Petrotympanicum. Sie schieben sich sogar zwischen das Petrotympanicum und die umgebenden Schädelknochen. Nach Reysenbach de Haan (1957) öffnet sich die Tuba auditiva tympanalwärts in den „pterygoid sinus"; bei den Mystacoceti verliert die Tube die Verbindung zur Bulla vollständig und endet in diesem Sinus.

Die Funktion der Luftsäcke bei den Walen wird in Zusammenhang mit der Notwendigkeit des Druckausgleiches beim Tauchen in große Tiefen gebracht. Dabei sollen sie, ähnlich wie der Mittelohrraum der Pinnipedia mit Schaum gefüllt sein. Soweit mir bekannt ist, liegen keine Beobachtungen an frischtoten Seekühen über etwaige Füllungen der Tympanalsäcke mit Schaum vor und auch die histologische Untersuchung ergab keinen dem „cavernous tissue" der Pinnipedia vergleichbaren, auffälligen Befund. D. P. Domning teilte mir mit, daß er bei der Sektion von gefrorenen oder fixierten Tieren keine Anhaltspunkte für eine Füllung des Cavum tympani mit Schaum erhielt. Eine weitere Funktion der Luftsäcke der Wale soll die akustische Isolation des Petrotympanicum sein (Fraser und Purves 1960). Für die Tympanalsäcke der Seekühe ist eine ähnliche Funktion erwägenswert. Der Schall wird beim Übertritt aus dem Wasser oder Gewebe in Luft zu 99,9 % reflektiert. Da der Gesang der Sirenen ein gleichzeitiges Hören erschweren, wenn nicht unmöglich machen würde, wäre es von Vorteil, ventral des Gehörorganes ein Luftkissen auszubreiten, das der Isolation gegen selbsterzeugte Laute dient. Interessanterweise beobachteten Bullock et al. (1982) die verhältnismäßig geringste Reaktion, wenn sie ihr Versuchstier von ventral akustisch reizten. Obwohl *Trichechus* nur in geringe Tiefen taucht, kann der Luftsack darüber hinaus auch für den Druckausgleich bestimmt sein, wofür das Auftreten von lockerem Füllgewebe zwischen Ramus mandibulae und Petrotympanicum spricht.

Eine besondere Schwierigkeit des Hörens unter Wasser ist es, eine Schallquelle zu

lokalisieren. Da sich der Schall im Wasser fast um das 4,5fache schneller ausbreitet als in der Luft und er ungehindert vom Wasser durch das Gewebe zum Innenohr gelangt, kann beispielsweise der Mensch unter Wasser keine Schallrichtung orten. Für ein aquatisch lebendes Tier sind zwei Lösungen dieses Problems denkbar. Entweder gelingt es, eine zeitliche Verzögerung zwischen dem Auftreffen des Schalls auf das linke und rechte Ohr zu erzeugen, was eine morphologische Lösung auf dem Niveau der Ohrregion erforderte, oder in den zugehörigen Gehirnzentren findet eine Auflösung des fast gleichzeitig auftretenden Schalls statt.

Der Abstand zwischen den beiden ovalen Fenstern beträgt bei einem uns vorliegenden Exemplar von *Trichechus* 8,5 cm. Berücksichtigt man den Faktor der Schallausbreitung im Wasser, so ergibt sich ein, einem terrestrischen Säugetier vergleichbarer, funktioneller Abstand von ungefähr 2 cm. Dies ist für kleinere Landsäugetiere kein ungewöhnliches Maß. Auf der Grundlage unserer Kenntnis über die akustischen Zentren im Gehirn der Sirenia ist es unmöglich, Aussagen über spezielle Anpassungen an die Schallortung zu treffen. Das Gehörorgan ist zentralnervös gut repräsentiert, denn im Gehirn *Dugong dugon* ist das Corpus geniculatum mediale mächtig entwickelt und auch die Colliculi caudales und die Olive scheinen, bezogen auf das Volumen des Gehirnes, vergrößert zu sein (Dexler 1913). Verhaart (1972) beschreibt die akustischen Zentren des Hirnstammes bei dieser Gattung als einigermaßen normal. Da ich keine morphologischen Besonderheiten gefunden habe, die auf eine Differenzierung der Schallrezeption hinweisen könnten, könnte eine neuroanatomische Untersuchung unter Umständen weitere Hinweise zur Lösung dieses Problems bringen.

Der Mangel an experimentellen Daten zur Schalleitung im Ohr der Seekühe, erlaubt nur vorsichtige, funktionelle Rückschlüsse zu diesem Problem aus den anatomischen Befunden. Die Untersuchungen von Fleischer (1971) zur Schalleitung wurden am mazerierten, trockenen und vom Schädel isolierten Petrotympanicum durchgeführt und haben damit nur bedingte Aussagekraft. Damit bleibt auch hier als einzige Möglichkeit, Analogieschlüsse zu den Verhältnissen bei Cetaceae und Pinnipedia zu ziehen. Doch begegnen wir sofort Schwierigkeiten, denn einerseits ist die Morphologie des Gehörorganes der Cetacea und Sirenia sehr verschieden, andererseits gibt es mindestens zwei kontroverse Ansätze zur Erklärung der Schalleitung bei Walen. Während eine Schule die Knochenleitung als Grundmechanismus annimmt (Norris 1968; McCormick et al. 1970), hält die andere eine Rezeption des Schalles auf dem auch für terrestrische Säugetiere üblichen Weg für wahrscheinlichs (Purves und Pilleri 1983).

Genau in der Frage, ob der Schall bei den Seekühen ungehinderten Zutritt zum Innenohr hat, oder ob dieses akustisch gegen den umgebenden Schädel isoliert ist, fehlt die empirische Grundlage. Bei Pinnipedia wird das Innenohr bis auf eine Verbindung zwischen Petrotympanicum und Squamosum entkoppelt (Repenning 1972). Wale haben die akustische Isolation optimiert, indem sich, wie erwähnt, Luftkissen zwischen das Petrotympanicum und die umgebenden Schädelknochen schieben. Bei Delphinidae und Phocaenidae wird das Petrotympanicum nur an Ligamenten aufgehängt (Robineau 1969). Am Schädel der Sirenia liegt die fast kugelige Fläche des Petrosum der entsprechenden Aushöhlung des Squamosum eng an. Fleischer (1978) nimmt an, daß sich dazwischen eine Knorpelschicht (S. 13) oder „elastic soft tissue" (S. 53) befindet. Nach experimentellen Befunden von Tonndorf et al. (1966) sind Diskontinuitäten zwischen Knochen keine reflektierenden Filter. Damit könnten die Bedingungen für die Weiterleitung von Schall durch die Schädelknochen zum Innenohr gegeben sein. Sofort stellt sich jedoch die Frage, welche Funktion das Trommelfell und die Gehörknöchelchen mit ihrer einzigartigen Morphologie besitzen, wenn sie nicht der Schallaufnahme und -leitung dienen.

Zum Abschluß der Diskussion über Probleme des Hörens bei Seekühen soll noch kurz auf eine von Fleischer (1978) erneut aufgestellte Hypothese eingegangen werden. Schon Lillie (1910) vermutete, daß bei den Walen die Bulla tympanica in Schwingung geraten

kann. Nach Fleischer ist bei den Sirenia und Cetacea das freischwingende Tympanicum neben Malleus/Incus und Stapes das dritte schalleitende Element. Hierdurch werde die Bandbreite der hörbaren Frequenz erweitert, wovon die Seekühe jedoch keinen Gebrauch machten. Daß diese Annahme ohne experimentelle Prüfung als Tatsache hingestellt wird, wurde schon von Lay (1980) bemängelt. Wie bereits ausgeführt, ist schon die Ansicht, die Gehörknöchelchen hätten beim Hören unter Wasser schalleitende Aufgaben, nicht unumstritten. Schließlich muß die Annahme eines freischwingenden Tympanicum bei *Trichechus* ebenfalls in Frage gestellt werden.

Fleischer (1978, S. 14) schreibt: „Looking first at the Sirenians, we see that the tympanic is still a u-shaped element fused with the periotic at both ends (Fig. 5)." In Wirklichkeit ist das Tympanicum nicht an seinen dorsalen Enden, sondern an der Medialseite durch zwei Knochenbrücken mit dem Petrosum verwachsen. Deshalb müssen sich von Fleischers Annahmen abweichende Schwingungsverhältnisse ergeben, wobei besonders zu berücksichtigen ist, daß eine Achse durch die ventralen Punkte der beiden Verbindungsbrücken noch unterhalb des ventralen Randes des Trommelfelles liegt. Ebenso bleibt bei allen diesen Überlegungen der Einfluß der umgebenden Weichteile unberücksichtigt.

Abkürzungen

Aaa – Arcus anterior atlantis, A. cco – A. carotis communis, A. cex – A. carotis externa, A. cin – A. carotis interna, A. max – A. maxillaris, A. sta – A. stapedialis, C. ary – Cartilago arytaenoidea, C. cri – Cartilago cricoidea, C. tra – Cartilagines tracheales, Co – Condylus occipitalis, Ct – Chorda tympani, D. art – Discus articularis, Dupl. – Duplikatur der Tympanalsackmembran, Eo – Exoccipitale, Epi – Epiglottis, G – Grenze zwischen Pars tensa und Pars flaccida, G. css – Ganglion cervicale superius nervi sympathicis, h. F. – hintere sichelförmige Falte, Hy – Hypophse, I – Incus, J – Jugale, L. apd – Lig. apicis dentis, M – Malleus, M. bra – M. brachiocephalicus, M. cap – M. cricoarytaenoideus posterior, M. cop – M. constrictores pharyngis, M. dig – M. digastricus, M. lca – M. longus capitis, M. lco – M. longus colli, M. mas – M. masseter, M. ptl – M. pterygoideus lateralis, M. ptm – M. pterygoideus medialis, M. rcv – M. rectus capitis ventralis, M. stm – M. sternomastoideus, M. stp – M. stylopharyngeus, M. tty – M. tensor tympani, M. tvp – M. tensor veli palatini, Mea – Meatus acusticus externus, Mm – Manubrium mallei, N. cin – N. caroticus internus, N. fac – N. facialis, N. las – N. laryngeus superior, N. lin – N. lingualis, N. mas – N. massetericus, N. ptm – N. pterygoideus medialis, Oes – Oesophagus, Opta – Ostium pharyngeum tubae auditivae, P – Petrosum, Pm – Palatum molle, R. man – Ramus mandibularis, R. pha – Ramus pharyngeus (N. vagus), S – Mediosagittalschnittebene, Sq – Squamosum, Sso – Synchondrosis sphenooccipitalis, St – Stapes, Sty – Stylohyale, T. sym – Truncus sympathicus, Tt – Tegmen tympani, Tym – Anulus tympanicus, Tys – Tympanalsack, V. jug – Vena jugularis, v. F. – vordere sichelförmige Falte, IX – N. glossopharyngeus, X – N. vagus, XI – N. accessorius, XII – N. hypoglossus.

Danksagung

Bei Herrn Prof. Dr. W. Maier und Herrn Prof. Dr. Dr. D. Starck, beide Frankfurt/M., möchte ich mich ausdrücklich für die vielen Diskussionen und die kritische Durchsicht des Manuskriptes bedanken. Frau Dr. G. Klauer, Frankfurt/M. danke ich herzlich für die Diskussion besonders der histologischen Befunde. Das Manuskript wurde kritisch von Frau Dr. E. Mickoleit, Tübingen, Herrn Dr. D. P. Domning, Washington, und Herrn Dr. G. Mickoleit, Tübingen, gelesen, wofür ich ihnen sehr danke. Der Zeichnerin des Zentrums der Morphologie in Frankfurt, Frau M. Roser, danke ich sehr herzlich für die mit großer Geduld und Können angefertigten Zeichnungen. Ebenso danke ich Frau U. Trautmann, Zentrum der Morphologie, und Herrn Dipl. Biol. E. Frey, Tübingen, für die photographischen Arbeiten. Frau U. Ruiter, Zentrum der Morphologie, danke ich für die Anfertigung der histologischen Schnitte.

Bei Herrn Prof Dr. Dr. D. Starck bedanke ich mich sehr für die Überlassung des wertvollen Materiales. Herrn Dr. R. K. Bonde vom U.S. Fish and Wildlife Service, Gainesville, Florida, möchte ich an dieser Stelle meinen verbindlichsten Dank für die hilfreiche Zusammenarbeit und Übersendung des juvenilen Tieres aussprechen. Dem Leiter der Zoologischen Schausammlung, Herrn Dr. G. Mickoleit, danke ich herzlich für die Möglichkeit, daß ich dort die Sektion des Tieres durchführen konnte.

Zusammenfassung

Die Weichteilanatomie des Gehörorganes von *Trichechus manatus* L. wird beschrieben. An den beiden untersuchten Exemplaren dieser Art endet der äußere Gehörgang in einem Blindsack, der nicht mit dem Trommelfell in Kontakt steht. Das vom Manubrium mallei zeltartig nach lateral vorgebuchtete Trommelfell wird von einer ungewöhnlich derben Bindegewebsplatte gebildet. Eine weitere Besonderheit des Mittelohres von *Trichechus* ist der Tympanalsack. Die eigentliche Paukenhöhle, nämlich der Raum zwischen Tympanalring und Petrosum, ist ventral zu einem geräumigen, membranösen Sack erweitert. Er dehnt sich zwischen Schädelbasis, Processus pterygoideus und Anulus tympanicus aus. Der Tympanalsack ist als Teil des Cavum tympani aufzufassen. Er wird wie dieses von einem mehrreihigen Flimmerepithel ausgekleidet. Die Tuba Eustachii weicht sehr von den üblichen Verhältnissen der Säugetiere ab; so tritt z. B. kein Tubenknorpel auf. Nach dem Vergleich des Tympanalsackes der Trichechidae mit den Luftsäcken (Diverticula tubae Eustachii) der Procaviidae, Equidae und Tapiridae ist eine Homologie der beiden Strukturen abzulehnen. Vorsichtige Überlegungen zur Funktion der Tympanalsäcke legen nahe, diese als Luftkissen anzusehen, die der Isolation gegen selbsterzeugte Laute dienen. Die Probleme des Richtungshörens unter Wasser und der Schalleitung werden auf die Verhältnisse der Seekühe bezogen und diskutiert.

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Z. Säugetierkunde 53 (1988) 380–381

ISSN 0044-3468

WISSENSCHAFTLICHE KURZMITTEILUNG

Home range of an African wildcat, *Felis silvestris* (Schreber), near Elmenteita, Kenya

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Receipt of Ms. 21. 02. 1988

The African wildcat (*Felis silvestris;* Honacki et al. 1982) is a common predator in the grasslands and woodlands of East Africa, but almost no quantitative information on its movements is available (Kingdon 1977; Smithers 1983). Here we describe the home range of a 3.7-kg male wildcat radiocollared near Elmenteita, Kenya (0° 30 ′ S, 36° 10 ′ E) during August 1987.

Temperatures in the area during the study period were warm during the day (13–21 °C) and cool at night (4–10 °C); rain was infrequent. Topography is generally flat except for a small, seasonally-dry river bed 5 m deep that bisected the cat's home range. Habitat types in the area included: Grassland (*Themeda triandra, Chloris gayana, Aloe* spp., and *Withania somnifera*), Agriculture (mostly maize fields), Open woodland (< 50 % tree and shrub cover with *Acacia xanthophloea, Euphorbia candelabrum, Opuntia vulgaris, Senecio petitianus, Cordia ovalis, Maerua triphylla,* and *Warbugia salutaris*), and Riverine woodland (> 50 % tree and shrub cover mainly with *Ficus sycomorus*).

The wildcat was captured in a padded steel foot-hold trap (Victor fox-sized "Soft-Catch", Woodstream Corp., Lititz, Pennsylvania, USA), then injected via hand-held syringe with a combination of 11 mg/kg ketamine hydrochloride (100 mg/ml; Ketaset, Birstol-Myers Co., Syracuse, New York, USA) and 5 mg/kg promazine hydrochloride (50 mg/ml; Sparine, Wyeth Laboratories, Inc., Philadelphia, Pennsylvania, USA). A 40-g radiocollar was fitted around the neck, and a numbered metal tag (3 × 12 mm) was affixed to each ear. Radiotelemetry locations were determined using a 3-element hand-held yagi antenna, usually while investigators were standing on the roof of a vehicle. The cat was seen once and was located from < 50 m away three other times. The other 13 radiolocations were determined through triangulation from an average of 2.2 bearings/location made 5 minutes apart, 0.5 km from the animal. Accuracy was estimated from 13 field tests with transmitters located at positions unknown to one investigator. Mean error of bearings was 6° (range = 0–14°), resulting in a calculated error of ± 52 m at a distance of 0.5 km. The capture location and 17 telemetry locations were plotted on a topographic map (1:25,000) and recorded as X-Y coordinates on the Universal Transverse Mercator Grid. Home range size was estimated by outlining the minimum perimeter polygon and calculating its area (Odum and Kuenzler 1955). Changes in signal strength caused by flexion of the antenna on the radiocollar indicated when the wildcat was active. Activity observations were recorded only once within any one hourly interval, sometimes even when a location was not recorded. Habitat distribution was drawn on a topographic map with the aid of aerial photos and ground investigations. Habitat occurrence within the home range was determined by placing a dot-grid over the map and calculating frequency of occurrence.

The wildcat was captured on 11 August 1987 and located 17 times during 12–27 August.

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Radiolocations were obtained more often between sunrise (0700 h) and sunset (1900 h) than at night (n = 11 and 6, respectively). Activity signals (n = 19) indicated that the cat was mostly nocturnal; all 10 signals obtained during 18000 to 0900 h indicated activity, vs. none of 9 obtained at other times. The wildcat's home range was estimated as 1.6 km^2. Habitat composition of the home range included open woodland (50 %), grassland used for cattle grazing (40 %), riverine woodland (5 %), and agriculture (5 %). The wildcat was located traveling in open grassland during at least 2 different nights, and apparently used different daytime resting sites on 8 of 9 days.

Smithers (1983) stated that African wildcats are almost entirely nocturnal, as we also observed. Wildcats in Europe are also active mostly at night, but sometimes cover long distances during the day (Artois 1985). Home ranges of wildcats in Europe were reported as 0.5 km^2 (Nowak and Paradiso 1983), and 0.6–0.7 km^2 (Leuw 1957 in Kingdon 1977). Radiocollared European wildcats had daily ranges of 0.3–3.3 km^2, and 1.8–12.7 km^2 over longer periods (Artois 1985; Stahl et al. 1988). Our estimate of home range size is likely minimal because our marked wildcat was monitored for only a short time. Wildcats have a wide habitat tolerance, but are conspicuous in open areas (Kingdon 1977) and require cover to rest in during the day (Artois 1985; Smithers 1983). These requirements were reflected in the mix of habitats occurring in the home range of the wildcat we monitored.

Acknowledgements

We gratefully acknowledge the financial and logistical support of the National Museums of Kenya, the Kenya Museum Society, the Minnesota Department of Natural Resources, B. van Valkenburgh and R. Wayne of University of California, Los Angeles, A. Walker of The Johns Hopkins University, Baltimore, and P. Behr of Delamere Estates, Ltd. G. Mungai of the National Museums of Kenya kindly identified plant specimens and D. Kuehn provided helpful comments on the manuscript.

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Ausschreibung des Fritz-Frank*-Preises
Förderpreis der Deutschen Gesellschaft für Säugetierkunde

Die Deutsche Gesellschaft für Säugetierkunde schreibt den Förderpreis in Höhe von 3000,– DM als Anerkennung für hervorragende wissenschaftliche Leistungen junger Forscher aus.

Voraussetzung ist eine im Druck vorliegende Arbeit aus den Gebieten Phylogenie und Systematik, Verbreitung, Ethologie, Ökologie oder Populationsbiologie der Säugetiere. Die Arbeit muß in den 3 vorausgehenden Kalenderjahren erschienen sein. Die Autoren dürfen beim Erscheinen der Arbeit nicht älter als 33 Jahre sein.

Bewerbungen oder Vorschläge erbitten wir an die Geschäftsstelle der Gesellschaft: Prof. Dr. U. Schmidt, Zoologisches Institut, Poppelsdorfer Schloß, D-5300 Bonn 1, unter Beifügung von 5 Sonderdrucken.

Der Jury gehören Wissenschaftler verschiedener Universitäten und Mitglieder der Gesellschaft an.

Der Preis wird bei der Eröffnung der Jahresversammlung der Gesellschaft in Lausanne (10.–14. 9. 1989) überreicht.

* Unser Mitglied, Herr Dr. Fritz Frank, ist am 3. 8. 1988 nach schwerer Krankheit verstorben. Über viele Jahre hinweg galt seine besondere Sorge dem wissenschaftlichen Nachwuchs. 1986 stiftete er den Förderpreis der Deutschen Gesellschaft für Säugetierkunde für die jungen Forscher.

Protokoll über die Mitgliederversammlung der Deutschen Gesellschaft für Säugetierkunde e.V. am 3. Oktober 1988 im Vortragssaal des Westfälischen Museums für Naturkunde in Münster

Der 1. Vorsitzende, Herr Kulzer, eröffnet die Versammlung um 17.30 Uhr.

1. Die Tagesordnung wird angenommen.
2. Herr Kulzer überreicht bei der Eröffnung der 62. Hauptversammlung den Förderpreis der Deutschen Gesellschaft für Säugetierkunde an Herrn Dr. V. Sommer.
   Der Vorstand hat beschlossen, den Preis künftig als „Fritz-Frank-Preis – Förderpreis der Deutschen Gesellschaft für Säugetierkunde" auszuschreiben.
3. Herr Schmidt verliest den Bericht über das abgelaufene Geschäftsjahr 1987:
   Im Berichtsjahr erschien der 52. Band der „Zeitschrift für Säugetierkunde" in sechs Heften mit 384 Seiten. Zusätzlich wurde allen Mitgliedern das Sonderheft mit den Kurzfassungen der Vorträge und Posterbeiträge der Tagung in Berlin zugesandt.
   Auf Einladung der Herren Klös, Frädrich und Niemitz fand die 61. Hauptversammlung der Gesellschaft vom 28. 9.–2. 10. 1987 in Berlin statt. Über 200 Tagungsteilnehmer besuchten die wissenschaftlichen Veranstaltungen. Erstmals wurde der Förderpreis verliehen, und zwar an Herrn Dr. Martin S. Fischer.
   Durch den Tod verlor die Gesellschaft folgende Mitglieder:
   Dr. Fritz Frank, Echterdingen,
   Dr. Friedrich Kühlhorn, München,
   Prof. Dr. Ulrich Lehmann, Köln.
   Im Jahr 1987 hatte die Gesellschaft 627 Mitglieder.

4. Frau Kühnrich verliest den Kassenbericht für das Geschäftsjahr 1987.
5. Die Kassenprüfer Herr Bohlken und Herr Schliemann haben keinen Anlaß zur Beanstandung gefunden. Sie sprechen die Empfehlung aus, daß die Mitgliederwerbung verstärkt wird und säumige Mitglieder auch die Mahngebühren zahlen müssen.
6. Die Anträge zur Entlastung des Schatzmeisters und des Vorstandes werden einstimmig angenommen.
7. Als Kassenprüfer für das Geschäftsjahr 1988 werden die Herren Bohlken und Schliemann wiedergewählt.
8. Der Vorschlag, die Mitgliedsbeiträge für Vollmitglieder auf DM 95,– zu erhöhen, Beiträge für Studenten (DM 60,–) und Ehegatten ohne Zeitschriftenbezug (DM 10,–) unverändert zu lassen, wird mit drei Enthaltungen angenommen.
9. Mit einer Enthaltung nehmen die Mitglieder die Einladung von Herrn Vogel an, die 63. Hauptversammlung vom 10.–14. September 1989 in Lausanne abzuhalten. Als Schwerpunktthemen werden „Wildlife-Management der Säugetiere", „Endokrinologie und Neurohormone der Säugetiere" und „Einsatz telemetrischer Methoden in der Säugetierforschung" gewählt. Die Einladung der Herren Schröpfer und Everts, 1990 in Osnabrück zu tagen, wird durch Akklamation angenommen.
   Für 1991 hat Herr Schliemann die Gesellschaft nach Hamburg eingeladen.
10. Der Versammlung wird bekanntgegeben, daß Frau Rasa in das Herausgeberkomitee der „Zeitschrift für Säugetierkunde" gewählt worden ist.
11. Es wird darüber diskutiert, wie man künftig Poster-Beiträgen zu größerer Wirksamkeit verhelfen kann.
12. Die Sitzung endet um 17.45 Uhr.

Prof. Dr. E. Kulzer, 1. Vorsitzender — Prof. Dr. U. Schmidt, Geschäftsführer — Dr. H. Frädrich, Schriftführer

Internationale Kommission für Zoologische Nomenklatur

The following opinions have been published by the International Commission on Zoological Nomenclature in the Bulletin of Zoological Nomenclature:

Vol. 44, parts 3 and 4, 1987

1460 *Dasyurus hallucatus* Gould, 1842 (Mammalia, Marsupialia): conserved

Vol. 45, part 3, September 1988

1516 *Taeniolabis* Cope, 1882 (Mammalia, Multituberculata): *Polymastodon taoensis* Cope, 1882 designated as the type species

1517 *Viverravus gracilis* Marsh, 1872 (Mammalia, Carnivora): generic and specific names conserved

GRZIMEK, B. (Hrsg.): **Grzimeks Enzyklopädie Säugetiere – Band 2.** München: Kindler Verlag 1988. 648 S., zahlreiche Abb., Lexikon-Großformat. Leinenausgabe: Subskriptionspreis 128,– DM, später 148,–, ISBN 3-463-42002-3; Luxusausgabe (Halbleder): Subskriptionspreis 168,–, später 198,–, ISBN 3-463-42102-X

Bereits kurze Zeit nach dem 4. ist nun Bd. 2 dieser neuen Enzyklopädie erschienen. Darin werden die Arten aus den Ordnungen Scandentia, Primates, Xenarthra und Pholidota behandelt. 29 sachkundige Autoren sind daran beteiligt. Die verschiedenen Kapitel zeigen entsprechend der grundsätzlichen Konzeption des Werkes gewisse Übereinstimmungen im Aufbau, indem sie mit Basisinformationen, einleitenden Kennzeichnungen systematischer Gruppen und tabellarischen Zusammenstellungen mehrerer biologischer Daten versehen sind. Die behandelten Arten werden von den verschiedenen Autoren zwar mit unterschiedlichen Schwerpunkten, jedoch recht ausführlich in ihrer Biologie charakterisiert. Die Tupaias, die neuweltlichen Edentaten und die Schuppentiere sind jeweils von 2 Autoren bearbeitet. Über bereits bekannte Sachverhalte hinaus findet der Leser sehr viele neuere Erkenntnisse integriert, vor allem über physiologische und Verhaltensbesonderheiten, ökologische Ansprüche und rezente Bestandssituationen. Die Bearbeitung dieser artenarmen Ordnungen macht zwar einen ausreichenden, jedoch vergleichsweise geringen Anteil am Umfang des Bandes aus. Der weitaus größte Teil bleibt, wie zu erwarten, den Primaten vorbehalten. Deren Artenvielfalt und Biologie werden entsprechend den Ergebnissen primatologischer Forschung besonders ausführlich behandelt. Informationen über anatomische und physiologische Besonderheiten, über Ökologie und Verhalten werden in erzählender und allgemein verständlicher Weise vermittelt, häufig werden soziale Organisationen und Gruppendynamik in besonderer Weise beschrieben. Den in natürlichen Beständen stark bedrohten Menschenaffen sind besondere Kapitel gewidmet. Zum Teil berichten mehrere Autoren hier aus eigener Erfahrung an Wildpopulationen über die gleiche Art. Probleme von Auswilderungen, in menschlicher Obhut nachgezogener Individuen und Maßnahmen zum Arten- und Biotopschutz werden an diesen Beispielen besonders eindrucksvoll geschildert. Auch dem Menschen ist ein umfangreicher Teil des Bandes gewidmet, insbesondere seiner Entstehungs- und Ausbreitungsgeschichte, seiner körperlichen Besonderheiten, Vielfalt und basalen Verhaltensweisen.

Beeindruckend sind auch in diesem Band die zahlreichen farbigen Situationsbilder von vielen Arten sowie Bildsequenzen von Bewegungsweisen. Dieser Band stellt eine ausgewogene und schöne Zusammenstellung über die heute bekannte Biologie der bearbeiteten Arten dar. Für Laien und Fachleute ist er eine vielfältige Informationsquelle.

D. KRUSKA, Kiel

GURAYA, S.: **Biology of Spermatogenesis and Spermatozoa in Mammals.** Berlin, Heidelberg, New York, London, Paris, Tokyo: Springer Verlag 1987. 430 pp., 85 figs. DM 298,–. ISBN 3-540-17143-6

Unsere Kenntnisse über die Biologie der Spermien und über die Spermatogenese sind in den letzten 20 Jahren auf Grund der Anwendung neuer Techniken, aber auch durch Integration der Ergebnisse verschiedener Disziplinen, enorm angewachsen. Das Schrifttumverzeichnis dieses Buches (53 Seiten) umfaßt, von ganz wenigen Ausnahmen abgesehen, fast nur Arbeiten seit 1960. Es handelt sich um einen umfassenden und detaillierten Bericht unter Berücksichtigung morphologischer (Ultrastruktur), histochemischer, biochemischer, immunbiologischer und physiologischer Aspekte vor allem auf molekularbiologischer Ebene. Da der Autor durch eigene Forschungen erheblich zum heutigen Kenntnisstand beigetragen hat, ist dies Buch weit mehr, als ein Sammelreferat. Zwei Hauptteile, Spermatogenese und Spermatozoa, sind in 12 Kapitel gegliedert. Als Beispiel sei der Abschnitt über SERTOLI-Zellen (20 Seiten) genannt, der eindrucksvoll belegen mag, wie die Einführung neuer Techniken und interdisziplinäres Denken es erreicht haben, daß Hypothesen durch sicheres Wissen ersetzt wurden. Von Interesse für den Säugetierforscher sind Hinweise auf die wesentliche Bedeutung von Zellstrukturen für die Systematik und Phylogenie. Für Veterinäre, Mediziner (Andrologie, Sterilitätsforschung) und Biologen ist das Werk von grundlegender Bedeutung.

D. STARCK, Frankfurt/M.

Erscheinungsweise und Bezugspreis 1988: 6 Hefte bilden einen Band. Jahresabonnement Inland: 308,– DM zuzüglich 13,80 DM Versandkosten, Gesamtpreis 321,80 DM einschließlich 7 % Mehrwertsteuer. Jahresabonnement Ausland: 308,– DM zuzüglich 18,– DM Versandkosten. Das Abonnement wird zum Jahresanfang berechnet und zur Zahlung fällig. Es verlängert sich stillschweigend, wenn nicht spätestens am 15. November eine Abbestellung im Verlag vorliegt. Die Zeitschrift kann bei jeder Buchhandlung oder bei der Verlagsbuchhandlung Paul Parey, Spitalerstraße 12, D-2000 Hamburg 1, bestellt werden. Die Mitglieder der „Deutschen Gesellschaft für Säugetierkunde" erhalten die Zeitschrift unberechnet im Rahmen des Mitgliedsbeitrages.

Z. Säugetierkunde 53 (1988) 6, 321–384




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